BEHAVIORAL AND BRAIN SCIENCES (2007) **30**, 63–134
Printed in the United States of America
DOI: 10.1017/S0140525X07000891

Consciousness without a cerebral cortex: A challenge for neuroscience and medicine

Bjorn Merker
Gamla Kyrkvagen 44, SE-14171 Segeltorp, Sweden
gyr694c@tninet.se

Abstract: A broad range of evidence regarding the functional organization of the vertebrate brain – spanning from comparative neurology to experimental psychology and neurophysiology to clinical data – is reviewed for its bearing on conceptions of the neural organization of consciousness. A novel principle relating target selection, action selection, and motivation to one another, as a means to optimize integration for action in real time, is introduced. With its help, the principal macrosystems of the vertebrate brain can be seen to form a centralized functional design in which an upper brain stem system organized for conscious function performs a penultimate step in action control. This upper brain stem system retained a key role throughout the evolutionary process by which an expanding forebrain – culminating in the cerebral cortex of mammals – came to serve as a medium for the elaboration of conscious contents. This highly conserved upper brainstem system, which extends from the roof of the midbrain to the basal diencephalon, integrates the massively parallel and distributed information capacity of the cerebral hemispheres into the limited-capacity, sequential mode of operation required for coherent behavior. It maintains special connective relations with cortical territories implicated in attentional and conscious functions, but is not rendered nonfunctional in the absence of cortical input. This helps explain the purposive, goal-directed behavior exhibited by mammals after experimental decortication, as well as the evidence that children born without a cortex are conscious. Taken together these circumstances suggest that brainstem mechanisms are integral to the constitution of the conscious state, and that an adequate account of neural mechanisms of conscious function cannot be confined to the thalamocortical complex alone.

Keywords: action selection; anencephaly; central decision making; consciousness; control architectures; hydranencephaly; macrosystems; motivation; target selection; zona incerta

1. Introduction

The four semi-independent pacemakers of the noncephalized nervous system of the cubomedusa equip this predatory jellyfish with flexible directional locomotor responsiveness to asymmetric sensory inputs (Satterlie & Nolen 2001). There is no reason to assume that the environmental guidance thus supplied by its radially arranged nerve net, involves or gives rise to experience of any kind. Our own environmental orientation, on the other hand, commonly takes place in a state of wakefulness we call conscious, which typically involves seeing, hearing, feeling, or other kinds of experience. Somewhere between medusa and human there is a transition to conscious function, and the nature of the capacity it bestows has exercised psychology, neuroscience, and cognitive studies virtually since their inceptions (Adrian et al. 1954; Baars 1988; James 1890/1983; Mandler 1975).

There is no compelling reason to think that nervous systems more complex than those of the medusa, and capable of performing more sophisticated functions, should not also perform in a perpetual night of unconsciousness. The fact that not all of them do so suggests that consciousness has some role or function to fill in the neural economy of brains thus endowed (Searle 1992). In exploring what this might involve, the exclusive concern throughout what follows will be with consciousness in its most basic and general sense, that is, as the state or condition presupposed by any experience whatsoever. Given recent proliferation of terminology surrounding the concept of consciousness (see Morin 2006 for a useful analysis and integration), the following additional remarks should help place this usage in context.

As employed here, the attribution of consciousness is not predicated upon any particular level or degree of complexity of the processes or contents that constitute the conscious state, but only upon whatever arrangement of those processes or contents makes experience itself possible. To the extent that any percept, simple or sophisticated, is experienced, it is conscious, and similarly for any feeling, even if vague, or any impulse to action, however inchoate.

BJORN MERKER is a neuroscientist with longstanding interest in brain mechanisms of consciousness: In an undergraduate term paper of 1971 he proposed the thalamic reticular nucleus as a central mechanism of attention on the basis of its anatomy and inhibitory connectivity. He obtained his doctorate from the Department of Psychology and Brain Science at M.I.T. in 1980 with a dissertation on the hamster colliculus. Since then he has worked on oculomotor physiology in cats, on the primary visual cortex in macaques, on song development and mirror self-recognition in gibbons, and on the evolutionary and developmental background to human music.

© 2007 Cambridge University Press 0140-525X/07 $40.00

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

This agrees well with the type of dictionary definition that renders consciousness as "the state or activity that is characterized by sensation, emotion, volition, or thought" (*Webster's Third New International Dictionary*, unabridged edition, 1961). In this basic sense, then, consciousness may be regarded most simply as the "medium" of any and all possible experience.

With regard to the way in which this medium might be implemented neurally, the present treatment is committed to an architectonic rather than a quantitative (or "graded") view. That is, as here conceived, a conscious mode of functioning is dependent upon quite specific neural arrangements creating interfaces of particular kinds between specific domains of neural function, rather than a result of a general increase in informational capacity or complexity achieved by expansion of a structural substrate which below a certain size does not support consciousness. Thus, what disqualifies the medusa nerve net in this regard is *not* its simplicity, but its lack of specific structural arrangements required to support conscious function. Given an arrangement capable of supporting consciousness, its contents may differ widely in complexity or sophistication. The range of possibilities in this regard is felicitously captured by the "scale of sentience" of Indian tradition (Bagchi 1975), as follows:

> "This."
> "This is so."
> "I am affected by this which is so."
> "So this is I who am affected by this which is so."

Each "stage" in this scale, from mere experienced sensation to self-consciousness, falls within the compass of consciousness as here defined, and presupposes it. Accordingly, to see, to hear, to feel, or otherwise to experience something is to be conscious, irrespective of whether in addition one is aware that one is seeing, hearing, and so forth, as cogently argued by Dretske (1993; see also Merker 1997; Searle 1992). Such additional awareness, in reflective consciousness or self-consciousness, is one of many contents of consciousness available to creatures with sophisticated cognitive capacities. However, as noted by Morin (2006), even in their case, it is present only intermittently, in a kind of time-sharing with more immediate, unreflective experience. To dwell in the latter is not to fall unconscious, but to be unselfconsciously conscious. Reflective awareness is thus more akin to a luxury of consciousness on the part of certain big-brained species, and not its defining property.

The exploration of the constitution of the conscious state to be pursued here will yield a conception of its functional role revolving around integration for action. As such, its functional utility will turn out to be independent of the level of sophistication at which the contents it integrates are defined. This opens the possibility that the evolution of its essential mechanisms did not have to await advanced stages of cortical development, but took place independently of it. As we shall see, certain fundamental features of vertebrate brain organization suggest that key mechanisms of consciousness are implemented in the midbrain and basal diencephalon, while the telencephalon serves as a medium for the increasingly sophisticated elaboration of conscious contents.

With some notable exceptions (e.g., Bogen 1995; Brown 1989; Panksepp 1982; Parvizi & Damasio 2001; Scheibel & Scheibel 1977; Sewards & Sewards 2000; Thompson 1993; Watt 2000), brainstem mechanisms have not figured prominently in the upsurge of interest in the nature and organization of consciousness that was ushered in with cognitivism in psychology and neuroscience (Baars 1988; Mandler 1975; Miller 1986). Few cognitivists or neuroscientists would today object to the assertion that "cortex is the organ of consciousness."[1] This is, in a sense, a return to an older view of the supremacy of the cerebral cortex from which a fundamental discovery of the late 1940s had stimulated a partial retreat. In keeping with the sense that the cerebral cortex is the organ of higher functions, it had been widely assumed that the regulation of its two primary states – sleep and wakefulness – was a cortical function, as well (see, e.g., the critical discussion of this stance in Gamper 1926, pp. 68–78). Then, in the late 1940s, Moruzzi and Magoun (1949) discovered that local stimulation of circumscribed cell groups in the pons and midbrain of experimental animals exerts a global activating influence on the cerebral cortex as well as on behavioral state, and that experimental lesions in these brainstem sites are capable of rendering animals somnolent and even comatose (Magoun 1954; cf. Parvizi & Damasio 2003). This came as a shock to the corticocentric perspective, and stimulated an avalanche of research on brainstem regulation of sleep and wakefulness and its relationship to the conscious state (summarized in symposium volumes edited by Adrian et al. 1954; Jasper et al. 1958; and Eccles 1966).

These efforts proved to be so successful that the once daring proposal that the brainstem regulates cortical state is unproblematic today. The same cannot be said of an allied, largely neglected, but even more radical proposal that emerged from the same pioneering wave of consciousness studies. Some of the principals in these developments – notably the neurosurgeon Wilder Penfield and his colleague Herbert Jasper – went on to re-examine the routine assumption that another "higher function," closely allied to that of sleep and wakefulness, namely consciousness, is an exclusively cortical affair (Penfield & Jasper 1954). On the basis of a set of clinical and physiological observations centered on the epilepsies, these authors proposed that *the highest integrative functions of the brain are not completed at the cortical level, but in an upper brainstem system of central convergence supplying the key mechanism of consciousness* (Penfield 1952). As their proposal is the natural point of departure for the present one, which elaborates and updates it in the light of subsequent developments, a brief review of its history follows.

2. Clinical beginnings

Penfield and Jasper left the anatomical definition of the upper brainstem system they invoked somewhat vague, but it was suggested to include the midbrain reticular formation and its extension into what was then known as the "nonspecific" thalamus (a nuclear grouping encompassing the midline, intralaminar, and reticular thalamic nuclei). They regarded this anatomically subcortical system to be functionally supra-cortical in the sense of occupying a superordinate position relative to the cerebral cortex in functional or control terms (Penfield & Jasper 1954,

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

pp. 28, 77; see sects. 3 and 4 of the target article following). They called it the "centrencephalic system," and assigned it a crucial role in the organization of conscious and volitional functions (ibid., p. 473). Figure 1 is based on a figure illustrating A. Fessard's lucid account of the conceptual setting for these ideas, included in the first of the symposium volumes cited earlier (Fessard 1954).

The Penfield and Jasper proposal emerged from extensive experience derived from an innovation in neurosurgical practice: they routinely removed sizeable sectors of cortex in conscious patients for the control of intractable epilepsy (Penfield & Jasper 1954). By performing the surgery under local anesthesia only, the authors ensured that their patients remained conscious, cooperative, and capable of self-report throughout the operation. This allowed the neurosurgeons to electrically stimulate the exposed cortex while communicating with the patient, in order to locate functionally critical areas to be spared when removing epileptogenic tissue. They then proceeded to remove cortical tissue while continuing to communicate with the patient. They were impressed by the fact that the removal of sizeable sectors of cortex such as those diagrammed in the composite of Figure 2 never interrupted the patient's continuity of consciousness even while the tissue was being surgically removed.

Penfield and Jasper note that a cortical removal even as radical as hemispherectomy does not deprive a patient of consciousness, but rather of certain forms of information, discriminative capacities, or abilities, but not of consciousness itself (Penfield & Jasper 1954, p. 477; cf. Devlin et al. 2003). That does not mean that no cortical insult is capable of compromising consciousness. In adult humans massive

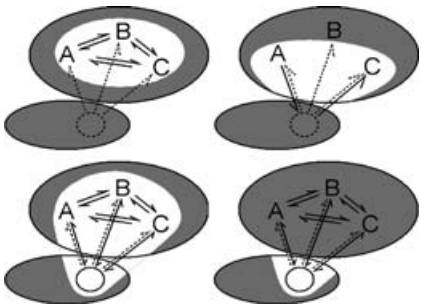


Figure 1. Four principal alternatives regarding interactions between cortex and brainstem in the constitution of the conscious state. Cortex (large oval) and brainstem (small oval) in highly schematic side (saggittal) view. Small circle: "centrencephalic system." In each alternative, normal waking cortical function is assumed to require "enabling" activation originating in the brain stem, marked by three dashed arrows radiating from brainstem to cortex. **Upper left**: the "corticocentric" alternative, in which integration through cortico-cortical connections alone is sufficient to constitute the conscious state. **Upper right**: Cortical integration via a subcortical relay, such as might occur via the dorsal thalamus. Only one such relay is depicted for the sake of clarity. The scheme is still corticocentric, since integration is cortical, albeit dependent upon extracortical relays for its implementation. **Lower left**: Centrencephalic hypothesis, based on diagram IV in Fessard (1954). Here an essential functional component of consciousness is supplied by brainstem mechanisms interacting with the cortex. **Lower right**: Primary consciousness implemented in the brainstem alone, as in cases of cortical removal or damage discussed in sections 4.4 and 5 of the text.

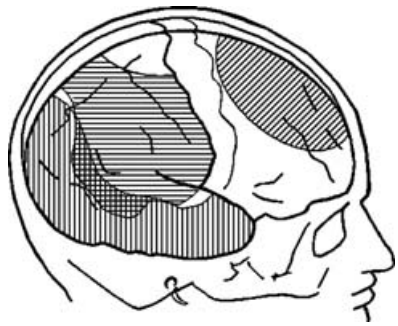


Figure 2. Large cortical excisions performed under local anesthesia by W. Penfield for the control of intractable epilepsy in three patients, entered on a single diagram. The patients remained conscious and communicative throughout the operation. All removals extended to the midline. The two posterior cases were right-sided, whereas the frontal removal was left-sided, and has been mirror-imaged. In no case was the removal of cortical tissue accompanied by a loss of consciousness, *even as it took place*. (Redrawn after figures VI-2, XIII-2, and XVIII-7 of Penfield & Jasper 1954.)

bilateral cortical damage will typically issue in a so-called persistent vegetative state (Jennett 2002). This by itself does not, however, allow us to make an equation between cortical function and consciousness, because such damage inevitably disrupts numerous brainstem mechanisms normally in receipt of cortical input, as discussed further in subsequent sections (see Shewmon 2004 for the conceptual and empirical complexities of the vegetative state). What impressed Penfield and Jasper was the extent to which the cerebral cortex could be subjected to acute insult without producing so much as an interruption in the continuity of consciousness. Their opinion in this regard bears some weight, in that their magnum opus of 1954 – *Epilepsy and the Functional Anatomy of the Human Brain* – summarizes and evaluates experience with 750 such operations.

When the exposed cortex was stimulated electrically to assess functional localization, stimulation parameters were adjusted so as to avoid triggering epileptic seizures in the patient. From time to time seizures were nevertheless triggered inadvertently. Over the large number of operations performed, every variety of seizure was thus produced by cortical stimulation, except one: Penfield and Jasper never saw the complete electrographic pattern that accompanies absence epilepsy induced by electrical stimulation of any part of the cerebral cortex (Penfield & Jasper 1954, p. 480). This pattern of 3 per second trains of "spike and wave" discharges evolves synchronously in the two hemispheres, down to a coincidence in the two hemispheres of the very first abnormal spike detectable in the electroencephalogram (Gibbs et al. 1936, 1937; Penfield & Jasper 1954, p. 483, Fig. XII-3, p. 624, Fig. XV-26, etc.).

Seizures of this type bear directly on our topic because of their conspicuous association with disturbances of consciousness (Penfield & Jasper 1954, pp. 24, 28). In fact, they are often *initiated* by a lapse of consciousness (p. 477), and in pure form they "consist almost solely of a lapse of consciousness" (p. 480). Without a preceding "aura" or other warning, and in the midst of normal activities, the patient assumes a vacant expression ("blank

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

stare") and becomes unresponsive. Ongoing activities may continue in the form of automatisms (as complex as automatic speech, implying organized cortical activity), or they may arrest for the duration of the often-brief seizure episode. At the end of such a seizure, which may last no more than a few seconds, the patient, who typically remains upright throughout, sometimes actively moving, resumes conscious activities where they were interrupted, has amnesia for what transpired during the episode, and may have no knowledge that the episode took place except indirectly, by means of evidence for the lapse of time available to the discursive, post-seizure, intellect.

Penfield and Jasper recognized in these seizures "a unique opportunity to study the neuronal substratum of consciousness" (Penfield & Jasper 1954, p. 480; cf. Blumenfeld & Taylor 2003). The coincident bilateral onset and cessation of these seizures suggested to the authors an origin in a centrally placed upper brainstem site of paroxysmal induction (Penfield & Jasper 1954, pp. 27, 473, 477, 482, 622–633). Though in their experience the pattern was not triggered by cortical stimulation, it could be evoked experimentally in the cat by stimulation of the midline thalamus (Jasper & Droogleever-Fortuyn 1947). Modern methods have added both detail and qualifications to the Penfield and Jasper account (see review by Meeren et al. 2005), yet upper brainstem involvement in absence epilepsy has stood the test of time, and is still being actively pursued both clinically and through research employing animal models (Blumenfeld & Taylor 2003; Danober et al. 1998; Derensart et al. 2001; McCormick & Contreras 2001; Stefan & Snead 1997; Strafstrom 2006). We shall return to this matter in Section 4.5.3.

Penfield and Jasper stressed that the postulated centrencephalic system is *symmetrically related to both cerebral hemispheres* (in the sense of radial rather than bilateral symmetry (see Penfield & Jasper 1954, p. 43, and figures on pp. 145 and 173). They denied that this system "functions by itself alone, independent of the cortex" and suggested instead that it "functions normally only by means of employment of various cortical areas" (Penfield & Jasper 1954, pp. 473–474). They conceived of it as a convergently innervated upper brainstem system serving to coordinate and integrate the functional economy of the forebrain as a whole, intimately involved in conscious and volitional functions, as well as in the laying down of memories across the lifespan (Penfield & Jasper 1954, pp. 140–145, 282).

3. Bringing the centrencephalic proposal up to date

A valuable review of the centrencephalic proposal, in light of developments up till the end of the 1980s, is provided by Thompson (1993, published posthumously). He calls attention to the relevance of the clinical literature on so called "subcortical dementia" to the centrencephalic theory, and further suggests that animal evidence for a subcortical "general learning system" may supply some of the anatomical detail left unspecified by Penfield and Jasper. This "general learning system" is defined by neural structures which, when damaged, produce deficits in *each* member of a set of highly diverse learning tests for rats. As identified through a long-term research program conducted by Thompson and colleagues, it consists of the basal ganglia, including the *substantia nigra* and ventral tegmental area, ventrolateral thalamus, superior colliculus, median raphé, and pontine reticular formation. The functional significance of key members of this constellation (which has access to sensory information independently of the cortex) is considered in some detail in Section 4 of the target article, for which the following preliminary considerations will set the stage.

The central claim of the Penfield and Jasper hypothesis is a claim regarding systems-level organization of neural functions. The idea that a system can be "anatomically subcortical but functionally supra-cortical" is a statement about brain macrosystems and how they relate and interact with one another. It is most easily approached from the side of the "final common path" of all brain output as far as actual behavior is concerned, namely brainstem and spinal motoneuron pools. Not only are these clusters of final output cells invariably innervated by multiple sources of afference (Graf et al. 2002; Kuypers & Martin 1982; Nudo & Masterton 1988; Ugolini 1995), but individual motoneurons receive synaptic input from diverse sources utilizing different transmitters (Holstege 1991; Wentzel et al. 1995). These sources include spinal and brainstem pattern generators (Grillner 2003), various territories of the brain stem reticular formation (Jordan 1998), and a multitude of both direct and indirect brainstem and forebrain afferents, among which the indirect ones often are relayed via the reticular formation (Zahm 2006).

Thus, the fact that the motor cortex maintains direct connections with brainstem and spinal motoneurons by no means implies that it ever is in sole command of behavior. At every level of its descending innervation of motoneuron pools it is only one of many inputs determining final outcomes. Moreover, the motor cortex accounts for just a fraction of descending cortical output, and is responsible for only select forms of distal behavior (Lang & Schieber 2003; Lawrence & Kuypers 1968; Kuypers 1982, 1987). In such a setting, the idea that the output of a subcortical structure might override a cortical one, and in this sense could exercise supra-cortical control over behavior, is hardly controversial. When an act of deliberate effort (say driven by prefrontal executive systems) is successful in overriding or inhibiting a given behavioral tendency, the cortex is in command of behavior, temporarily exercising determining control over its course. The fact that such effort does not always succeed (say in the face of sufficient magnitudes of fear, hunger, or pain) means that the frontal executive can be overridden by more primitive mechanisms. When a subcortical source prevails in such competitive interactions, an anatomically subcortical system has exercised supra-cortical functional control over behavior.

It is necessary, in other words, to distinguish "higher" in the sense of cognitive sophistication from "higher" in control terms. In this light, the Penfield and Jasper proposal amounts to a claim that certain upper brainstem systems in receipt of convergent cortical projections occupy a superordinate position in the latter sense. As I detail further in subsequent sections, the diverse hemispheric as well as brainstem input to these structures equips them for the kind of superordinate decision

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

making crucial for the global sequencing and control of behavior (Prescott et al. 1999). It is also within processes dedicated to "integration for action" that we can find a well-defined functional role for a particular mode of neural organization that qualifies as conscious, in good agreement with the Penfield and Jasper proposal. To set the stage for a treatment of that more demanding topic in sections 4 and 5, two lines of evidence regarding brainstem function that bear on their proposal are briefly reviewed.

3.1. The Sprague effect

Complete removal of the posterior visual areas of one hemisphere in the cat (parietal areas included) renders the animal profoundly and permanently unresponsive to visual stimuli in the half of space opposite the cortical removal (Sprague 1966; see also, Sherman 1974; Wallace et al. 1989). The animal appears blind in a manner resembling the cortical blindness that follows radical damage to the geniculostriate system in humans. Yet inflicting *additional* damage on such a severely impaired animal at the midbrain level *restores* the animal's ability to orient to and to localize stimuli in the formerly blind field (Sprague 1966; cf. Sherman 1977; Wallace et al. 1989). This is accomplished by removing the contralateral superior colliculus or by an intervention as small as a knife-cut that severs fibers running in the central portion of the collicular commissure. That is, adding a small amount of damage in the brainstem to the cortical damage "cures" what appeared to be a behavioral effect of massive cortical damage. The restored visual capacity is limited essentially to the ability to orient to and approach the location of moving visual stimuli in space (Wallace et al. 1989). Visual *pattern* discrimination capacity does not recover after the midbrain intervention (Loop & Sherman 1977), though the midbrain mechanism can be shown to play a role even in such tasks (Sprague 1991).

The Sprague effect is a consequence of secondary effects generated at the brainstem level by the unilateral cortical removal (Hikosaka & Wurtz 1989; Hovda & Villablanca 1990; Jiang et al. 2003). The damage not only deprives the ipsilateral superior colliculus of its normal and profuse cortical input (Berson & McIlwain 1983; Harting et al. 1992; Palmer et al. 1972; Sprague 1975), but it unbalances collicular function via indirect projection pathways. Chief of these is the powerful inhibitory projection from the substantia nigra to the colliculus, which crosses the midline in a narrow central portion of the collicular commissure (McHaffie et al. 1993; Sprague 1996; Wallace et al. 1990; for additional possibilities, see Durmer & Rosenquist 2001). The "restorative" interventions partially correct this imbalance, allowing the collicular mechanism to resume at least part of its normal functional contribution to behavior, with partial restoration of visually guided behavior as a result.

The point is underscored by the analogous circumstances pertaining to the neglect of one half of space (unilateral neglect) that follows more limited inactivation of the cortex (by reversible cooling) at the junction of occipital, parietal, and temporal lobes in one hemisphere of the cat. This neglect also lifts upon inactivation (by reversible cooling) of the superior colliculus opposite to the cortical inactivation (Lomber & Payne 1996). Analogous restorative effects of midbrain damage on neglect caused by frontal cortical damage have been observed in a human patient (Weddell 2004). Though the unawareness featured in cases of unilateral neglect in humans is far from a simple entity (see review by Mesulam 1999), it bears on our topic by being perhaps the closest approximation to an impairment that includes specific effects on consciousness produced by localized cortical damage (Driver & Vuilleumier 2001; Rees 2001; see also Jiang et al. 2003).

The Sprague effect demonstrates that hidden in the hemianopia or neglect caused by cortical damage lies a deficit on the part of a brainstem visual mechanism disabled as a secondary effect of the cortical removal. This means that a functional deficit following damage limited to the cortex cannot, as a matter of course, be taken to reflect an exclusively cortical contribution to functional capacity, because the deficit may reflect "remote" effects on brainstem systems, as well. As Sprague originally expressed it:

> The heminanopia that follows unilateral removal of the cortex that mediates visual behavior cannot be explained simply in classical terms of interruption of the visual radiations that serve cortical function. Explanation of the deficit requires a broader point of view, namely, that visual attention and perception are mediated at both forebrain and midbrain levels, which interact in their control of visually guided behavior. (Sprague 1966, p. 1547)

That conclusion agrees well with the Penfield and Jasper perspective reviewed in the foregoing; and it tells us that without cognizance of potential subcortical contributions to a deficit caused by cortical damage, the scope of functions attributed to the cortex will be counterfactually inflated.

3.2. Target selection in the midbrain

Although superficially inconspicuous, the superior colliculus in the roof ("tectum") of the midbrain exhibits considerable structural and functional complexity. Long known to play a role in "visual grasping" or "foveation" (Hess et al. 1946; Schiller & Koerner 1971), further study has revealed unexpected sophistication in its functional organization (Keller et al. 2005; Krauzlis et al. 2004; May 2005; Sparks 1999). It is the only site in the brain in which the spatial senses are topographically superposed in laminar fashion within a common, premotor, framework for multi-effector control of orienting (Merker 1980). Its functional role appears to center on convergent integration of diverse sources of information bearing on spatially triggered replacement of one behavioral target by another, and evidence is accumulating for a collicular role in target selection (Basso & Wurtz 1998, 2002; Carello & Krauzlis 2004; Cavanaugh & Wurtz 2004; Fecteau & Munoz 2006; Glimcher & Sparks 1992; Horowitz & Newsome 1999; Krauzlis et al. 2004; McPeek & Keller 2004; Schlag-Rey et al. 1992; Wurtz & Mohler 1974; see also Grobstein 1988, pp. 44–45). Such a role has direct implications for the topic of superordinate control functions.

A collicular role in target selection is unlikely to be a passive reflection of decisions taken in other structures. It is not fully accounted for by the powerful input it receives from the substantia nigra (Basso & Wurtz

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

2002), and the diversity of collicular afferents precludes any one of them from exercising sole control over collicular function. These afferents include a wide range of brainstem (Edwards 1980; Edwards et al. 1979) and visual as well as nonvisual cortical sources (Collins et al. 2005; Harting et al. 1992; 1997; Kawamura & Konno 1979; Sherman et al. 1979). Cortical afferents are monosynaptic, originating in layer V pyramidal cells, placing the colliculus as close to the cortex as two cortical layers are to one another. In the cat they include some 17 visual areas (Harting et al. 1992), and in primates there are contributions from both the dorsal (parietal cortex) and the ventral (temporal cortex) "streams" of the visual system (Fries 1984; Steele & Weller 1993; Webster et al. 1993). Any sensory modality used in phasic orienting behavior appears to receive obligatory representation in the colliculus. Besides the major spatial senses of vision, audition, and somesthesis, they include pain (Wang & Redgrave 1997) and exotic senses such as infrared (Hartline et al. 1978), electroceptive (Bastian 1982), magnetic (Nemec et al. 2001), and echolocation systems (Valentine & Moss 1997), depending on species.

In the colliculus these diverse convergent inputs are arranged in topographically organized sheets layered one upon the other through the depths of the colliculus (Harting et al. 1992; May 2005). Intrinsic collicular circuitry distributes excitatory as well as inhibitory collicular activity within and across layers and across major collicular subdivisions (Behan & Kime 1996; Bell et al. 2003; Binns 1999; Doubell et al. 2003; Lee et al. 1997; Meredith & King 2004; Meredith & Ramoa 1998; Mize et al. 1994; Özen et al. 2000; Zhu & Lo 2000). There is therefore no dirth of complex intrinsic collicular circuitry – only beginning to be systematically charted – for collicular decision-making based upon its diverse sources of afference.

The collicular role in target selection is accordingly likely to be causal (Carello & Krauzlis 2004; McPeek & Keller 2004; see also Findlay & Walker 1999; Yarrow et al. 2004; and sect. 4.2 of the target article). This would place the colliculus at the functional top rather than bottom of control processes in its domain. The selection of a target for behavior is the brain's final output in that regard. It is the pivotal event for which all other processes are but a preparation, summing them up in the actual decision to settle on one target for action rather than another (Allport 1987; Brooks 1994; Dean & Redgrave 1984; Isa & Kobayashi 2004; McFarland & Sibly 1975; Tyrrell 1993; see Fecteau & Munoz 2006 for collicular "priority mapping" in relation to action).

The functional prediction from the loss of such a structure is not the absence of target acquisition, but its impoverishment. Not only is the brain redundantly organized in this regard (Lomber et al. 2001; Schall 1997; Schiller et al. 1979; Tehovnik et al. 1994), but the loss of a superordinate function in a layered control architecture does not disable the system as a whole (Brooks 1986, 1989; Prescott et al. 1999), just as a well organized army need not cease functioning on the loss of its commander. A macaque with experimental collicular lesions is not incapable of moving its eyes onto targets, but exhibits a reduced variety of eye and orienting movements and is indistractible, a common finding in other species as well (Albano & Wurtz 1978; Casagrande & Diamond 1974; Denny-Brown 1962; Goodale & Murison 1975; Merker 1980; Mort et al. 1980; Schiller et al. 1979; Schiller & Lee 1994; Schneider 1967). This may reflect a compromised *scope* and *sophistication* of target selection, and the role of the intact colliculus would accordingly instantiate the Penfield and Jasper conception of a *highest integrative function* which, while *anatomically subcortical*, is *functionally supra-cortical*.

4. Integration for action

As noted in section 3, in drawing the contrast between "higher" in cognitive terms and "higher" in control terms, competition for control over behavior ends only at the stage of the "final common path" of motoneurones. It is along that approach, among upper brainstem mechanisms of "integration for action," that we shall identify a prototype organization for conscious function. The issue takes us to the very origin of the vertebrate brain plan, which is not only cephalized, but centralized. Not all animals rely on centralized neural organization to control behavior, even when possessed of a brain. A number of invertebrate forms, including insects, concentrate considerable neural resources to segmental ganglia. Their brain is in a sense no more than the anterior-most of these ganglia, in receipt of the output of the specialized receptors of the head. It does not necessarily exercise a command function in the sense of central control of behavior (see Altman & Kien 1989).

The decentralized neural control of an insect such as the ant allows its body to survive without its brain. Moreover, if given adequate somatic stimulation in this condition, it will perform many of the complex behaviors in its repertoire with apparent competence, though naturally without relation to the distal environment (Snodgrass 1935). A vertebrate, on the other hand, does not survive for more than seconds after the loss of its brain, because in vertebrates even vital functions are under central brain control. The difference with respect to insects is underscored by the contrasting disposition of motor neurons. In insects, they are concentrated to segmental ganglia but are rare in the brain (Snodgrass 1935), whereas in vertebrates they populate the brain in sets of distinctively organized motor nuclei. Motor control in vertebrates has "moved up," as it were, to that end of the neuraxis which leads in locomotion and is in receipt of the output of the chief exteroceptors (cf. Grillner et al. 1997).

The basic organizational features of the vertebrate brain are highly conserved across taxa despite unequal development of one or another of its senses or subdivisions (Nieuwenhuis et al. 1998). All vertebrates, that is, have "in outline" the same brain plan, assembled from primitive beginnings in chordate ancestry (Butler & Hodos 1996; Holland & Holland 1999; Northcutt 1996b). The prominent role of large, image-forming eyes and their central connections in this development came to exert a profound effect on the manner in which the vertebrate brain plan was centralized, with implications for our understanding of the way in which "higher" in cognitive terms relates to "higher" in control terms. That development involves the integrative machinery straddling the so-called synencephalon, or junction between midbrain and diencephalon – to which we now turn.

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

4.1. The synencephalic bottleneck and how the vertebrate brain came to be centralized around it

There was a time in prevertebrate ancestry when the midbrain and diencephalon alone, or rather the first rostral differentiations of the neural tube that can be homologized with the vertebrate midbrain and diencephalon, constituted the functionally highest and also anatomically most rostral subdivision of the neuraxis (Holland & Holland 1999, 2001; Holland et al. 1994; Lacalli 1996, 2001; Wicht 1996). It housed the neural circuitry connecting a primitive, unpaired "frontal eye" and other rostral sensory equipment (Lacalli 1996) with premotor cells in cephalochordate filter feeders (represented today by *Amphioxus*, the lancelet). As far as is known, cephalochordate filter feeders lacked a sense of smell, and they were without a telencephalon altogether (Butler 2000; Holland et al. 1994).

Though our brain nomenclature historically groups the diencephalon together with the telencephalon to make up the forebrain, there is nothing fundamental about such a grouping, as the just mentioned phylogenetic circumstances show. Rather, for what follows it will be convenient to retain the primitive grouping of midbrain and diencephalon together under the label mesodiencephalon or "optic brain." In all vertebrates these two segments of the neuraxis, along with the transitional "synencephalon" (pretectum) wedged between them, house the primary terminations of the optic tract (cf. Butler 2000). The latter covers their external surfaces in the form of a ribbon of fibers running obliquely from the optic chiasm beneath the hypothalamus across the diencephalon and mesencephalon up to the latter's roof ("tectum"). Along the way it innervates structures as different as the hypothalamus, ventral thalamus, dorsal thalamus, pretectum, accessory optic nuclei, and superior colliculus (tectum). The same territory also houses some of the major *integrative structures of broad functional scope common to all vertebrates* (see Fig. 3).

The principal poles of this integrative machinery are the hypothalamus forming the floor of the diencephalon, on the one hand, and the superior colliculus forming the roof of the midbrain, on the other. The former is an intricate nuclear aggregate critical for the mutual regulation and integration of a vertebrate's entire repertoire of goal-directed, motivated behavior covering exploratory, foraging, ingestive, defensive, aggressive, sexual, social, and parental modes of behavior (Swanson 2000), to name the principal ones. The other pole, colliculus/tectum, serves the intermodal integration of the spatial senses by which vertebrates relate to their surroundings via coordinated orienting movements of eyes, head, and body, as already summarized in section 3.2. Between these two is wedged additional integrative machinery in the form of the midbrain reticular formation, ventral thalamus, the periaqueductal gray, the ventral tegmental/substantia nigra pivot of the striatal system, as well as "locomotor centers" and basic mechanisms serving navigation. I will return to some of these in subsequent sections.

This concentration of conserved integrative machinery to the mesodiencephalon, I suggest, reflects the costs and benefits of evolving image-forming eyes in the ancestors of vertebrates (cf. Northcutt 1996a). Full use of the potential powers of visual guidance meant evolving

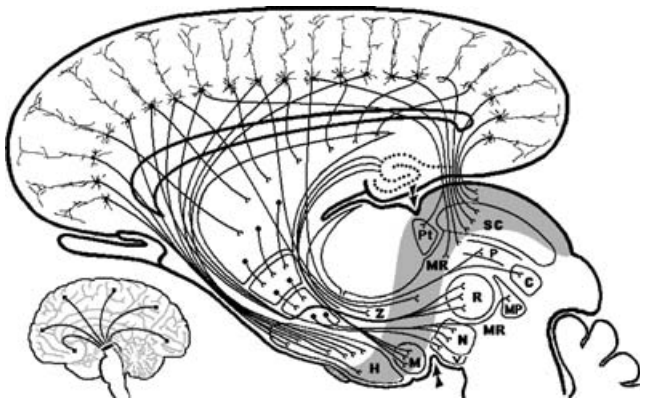


Figure 3. Schematic saggittal diagram depicting cortical convergence (in part via the basal ganglia) onto key structures in the region of the "synencephalic bottleneck" (marked by thick arrows in the main figure and by a black bar in the inset). Abbreviations: **C**, nucleus cuneiformis; **H**, hypothalamus (preoptic area included); **M**, mammillary bodies; **MP**, "mesopontine state control nuclei" (locus coeruleus, pedunculopontine and laterodorsal tegmental nuclei, and dorsal raphé); **MR**, midbrain reticular formation; **N**, substanta nigra; **P**, periaqueductal gray matter; **Pt**, pretectum; **R**, red nucleus; **SC**, superior colliculus; **V**, ventral tegmental area; Z, zona incerta. The dual axon seen issuing from some of the pyramidal cells of cortical layer 5 is an illustrative convenience only. Shaded region marks the surface course of the optic tract.

solutions to an intricate set of sensorimotor problems. The confounding of sensory information by the sensory consequences of movement ("re-afference"; von Holst & Mittelstaedt 1950) is particularly problematic for image-forming eyes, requiring their stabilization with respect to the world during movement. This is done by vestibular counter-rotation punctuated by quick resets of the eyes, which concentrates blurring-time to the brief reset episodes. Thus, *vision alone among all the senses features independent spatial mobility of the receptor array itself*, and a full-fledged oculomotor system evolved in the immediate ancestors of true vertebrates (Braun 1996, p. 272; Fritsch et al. 1990; Wicht 1996, p. 253). The reflex circuitry connecting vestibular and oculomotor nuclei, centered on the medial longitudinal fasciculus, is also among the most conservative and basic features of the brainstem in all vertebrates (Carpenter 1991; Windle & Baxter 1936).

Yet, with eyes free to turn in their orbits, there is no longer a fixed relation between retinal location and spatial direction relative to body or head, nor to the localizing function of any sensory modality which (in whole or in part) bears a fixed relation to the head. Hence the need for intermodal integration, for which the sensory integrating mechanism of colliculus/tectum – present in the roof of the midbrain of even jawless vertebrates – provides the basic, early and conserved solution (Iwahori et al. 1999; Zompa & Dubuc 1996). But once these basic problems of vision were solved, a bonus was within reach: Mobile eyes present a highly efficient means for sampling the environment, provided their control can be linked to motivational mechanisms ensuring their appropriate deployment in accordance with shifting needs.

It appears, in other words, that as the vertebrate brain plan took shape in prevertebrate ancestry under pressure of the evolution of mobile, image-forming eyes, a central

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

association between optic control circuitry and major neural mechanism for the integration of behavior/action were forged in segments of the neuraxis covered and innervated by the optic tract (cf. Fig. 3). At the time when this optic orienting machinery and associated integrative mechanisms evolved, the forebrain was still dominated by olfaction (Braun 1996; Northcutt & Wicht 1997; Wicht & Northcutt 1992). The sense of smell added no fundamentally new control requirements comparable to those of vision, and olfaction accordingly could be integrated with the mesodiencephalic control system by caudally directed fiber projections. These simply happen to arrive at the "optic brain" from an anterior direction, whereas other sensory afferents reach it from a caudal direction (somatosensory, octavolateral, i.e., vestibular/auditory/lateral line/electrosensory, etc.), or directly "from the side" through the optic tract (cf. Butler 2000).

Indeed, however much the telencephalon subsequently expanded, even to the point of burying the mesodiencephalon under a mushrooming mammalian neocortex, no other arrangement was ever needed, and that for the most fundamental of reasons. No efferent nerve has its motor nucleus situated above the level of the midbrain. This means that the very narrow cross-section of the brainstem at the junction between midbrain and diencephalon (synencephalon, marked by arrows in the main part of Fig. 3 and by a black bar in the inset) carries the total extent of information by which the forebrain is ever able to generate, control, or influence behavior of any kind. If, therefore, integration is for action, as proposed here for the mesodiencephalic control system, information-theory poses no obstacle to having an expansive neocortex make its contribution in this regard by convergent projections onto the highly conserved and pre-existing machinery of the midbrain and basal diencephalon, which therefore could retain its old integrative functions (see Fig. 3). Indeed, a bottleneck of this kind is exactly what is needed in order to convert the massively parallel and distributed information capacity of the cerebral hemispheres into a limited-capacity, sequential mode of operation featured in action selection for coherent behavior (Allport 1987; Baars 1993; Cabanac 1996; Cowan 2001; Mandler 1975; 2002, Ch. 2; McFarland & Sibly 1975; Tyrrell 1993).

That is, one need not know anything more about the vertebrate brain than the fact that its most rostral motoneurons are located *below* the synencephalic bottleneck, to know that the total informational content of the forebrain must undergo massive reduction in the course of its real-time translation into behavior. In the setting of such obligatory "data reduction" in a stretch of the neuraxis hosting major systems for the global regulation of behavior, a so far unrecognized optimizing principle lies hidden in the mutual dependency that links the motivational, the sensory, and the action selection requirements of the brain's control tasks. They form a "selection triangle," the principle of which is introduced here for the first time. The efficient neural implementation of this principle may harbor the secret of conscious function itself.

4.2. The "selection triangle": A proposed key to conscious function

Elementary necessities of animal existence such as food, shelter, or mates are not typically found in the same place at any given time, and they each require different and often incompatible behaviors. An animal's activities accordingly unfold under constraint of multiple goals or motives derived from the evolved and acquired needs it must fill through the sequence of its diverse actions over time (Baerends 1976; Tinbergen 1951). The tasks set by these goals compete for an animal's behavioral resources, and because the actions by which they are implemented are always confined to the present (where they typically are executed one at a time), their scheduling (action selection) features perpetual trade-offs in the time and effort that is allocated to them (McFarland & Sibly 1975). The ethological insight, that animal behavior rests upon a foundation of diverse goal functions that sometimes entail incompatible tasks or behaviors requiring sequencing/selection, entered the so-called behavior-based approach to robotics under the name "action selection" (Blumberg 1994; Brooks 1986; McFarland & Houston, 1981; Maes 1990; Prescott et al. 1999; Tyrell 1993; see also Meyer & Wilson 1991).

The needs reflected in the time budget of an animal's task allocations are, however, only one side of the equation of efficient decision-making. The fulfillment of needs is contingent on available *opportunities*. These are scattered in the world as ever-shifting targets of approach and avoidance among lively and often unpredictable contingencies within which they must be detected, located, and identified, often among multiple competing alternatives, all in real time. Interposed between the needs and their fulfillment through action on the world is the body with its appendages and other resources for getting about in the world and manipulating its objects. In concrete terms an action is a time series of bodily locations and conformations. These are what connect needs with opportunities. In so doing they themselves become a factor in singling out a given opportunity (target) for action (target selection). This is so because determining which one of several available potential targets is the best current choice for action will often depend, not on current needs alone, but additionally on the disposition of the body relative to those targets (in terms of its posture and position, movement trajectory, energy reserves, etc.; cf. Körding & Wolpert 2006).

In principle, each of the decision domains just invoked – action selection, target selection, and motivational ranking – may be defined in its own terms, without regard to the others. They may even make their contributions to behavior independently of one another (Altman & Kien 1989; Brooks 1986). But from the inherent functional relationship just sketched, that is, the fact that in terms of optimal performance *target selection is not independent of action selection, and neither of these is independent of motivational state* (reflecting changing needs), it follows that savings are achievable by exploiting that triangular dependency. It is not possible to reap the benefits of those savings short of finding some way of interfacing the three state spaces – each multidimensional in its own right – within some common coordinate space (decision framework) allowing their separate momentary states to interact with and constrain one another. This extends to such a tripartite interaction the principle already derived for the efficient management of motivational trade-offs, namely, the convertibility of different motives through a motivational "common currency"

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

and their convergence among themselves at some point in the system (McFarland & Sibly 1975; see also Cabanac 1992, and further in the present article).

The principle of a centralized brain system dedicated to this decision domain follows from this, though not the particulars of the three-way interface that must form its centerpiece. Evolving such an interface is far from a trivial problem, all the more so since its decisions must be made in real time. The brain, of course, has no direct access to either the target states of the world or the action states of the body that must be compared and matched in the light of motivational priorities. It is saddled with an inverse problem on both sensory and motor sides of its operations (Gallistel 1999; Kawato et al. 1993). The indirect reflections of relevant parameters to which it does have access, come to it, moreover, in diverse data formats. The differences between the spatial senses among themselves in this regard are mild compared to those between any one of these senses and the various musculoskeletal articulations and configurations they serve to control. How then might the former be compared with the latter? Add to this the already mentioned circumstance that every movement confounds the sensory information needed to guide behavior, and that the needs to be taken into account differ not only in urgency, but in kind, and the size of the design problem begins to emerge in outline.

To exploit the savings hidden in the functional interdependence between target selection, action selection, and motivation, this confounded complexity must be radically recast, to allow the three domains to interact directly in real time for the determination of "what to do next." It is the principal claim of the present target article that the vertebrate brain incorporates a solution to this decision problem, that it takes the general form of a neural *analog reality simulation* of the problem space of the tripartite interaction, and that the way this simulation is structured constitutes a conscious mode of function. It equips its bearers with veridical experience of an external world and their own tangible body maneuvering within it under the influence of feelings reflecting momentary needs, that is, what we normally call reality.[2] To this end it features an analog (spatial) mobile "body" (action domain) embedded within a movement-stabilized analog (spatial) "world" (target domain) via a shared spatial coordinate system, subject to bias from motivational variables, and supplying a premotor output for the control of the full species-specific orienting reflex. The crucial separation of body and world on which this arrangement hinges has recently been worked out in formal terms by David Philipona and colleagues (Philipona et al. 2003; 2004).

We have already seen in sections 3.2 and 4.1 that the roof of the midbrain of vertebrates houses a sophisticated laminar superposition of the spatial senses in a premotor framework for orienting. It appears to contain the essential signals for bringing these senses into registry (Groh & Sparks 1996; Jay & Sparks 1987; Krauzlis 2001; Populin & Yin 1998; Van Opstal et al. 1995; Zella et al. 2001) and for stabilizing the world relative to the body. Such stabilization is likely to utilize not only vestibular information (Bisti et al. 1972; Horowitz et al. 2005), but cerebellar "decorrelation" as well (Dean et al. 2002; 2004; cf. Guillaume & Pélisson 2001; Hirai et al. 1982; May et al. 1990; Niemi-Junkola & Westby 2000). The layered spatial maps in the roof of the midbrain would, in other words, represent the vertebrate brain's first bid for an analog simulation of a distal "world" (Scheibel & Scheibel 1977). We also saw that the other pole of the "optic brain," the hypothalamus, houses the basic circuitry for regulating and integrating motivational states related to goal-directed behaviors. Its output is brought to bear on the intermediate and deep layers of the superior colliculus not only by direct projections (Beitz 1982; Rieck et al. 1986), but indirectly, via massive and organized projections from hypothalamic nuclei to different sectors of the periaqueductal gray substance (Goto et al. 2005; see refs. 36, 37, 39, 222, & 256 in Swanson 2000).

The periaqueductal gray is a midbrain territory intimately related to the deeper collicular layers. It surrounds the cerebral aqueduct, and plays a critical role in the expression of a variety of emotion-related behaviors such as defensive, aggressive, sexual, vocal, and pain-related ones (Adams 1979; Behbehani 1995; Fernandez de Molina & Hunsperger 1962; Holstege et al. 1996; Jurgens 1994; Kittelberger et al. 2006; Lonstein et al. 1998; Mouton 1999; Panksepp 1982; 1998a; Watt 2000). Its longitudinal columns are functionally organized in terms of high-level tasks, goals, strategies, or contexts, such as "inescapable versus escapable pain" (Keay & Bandler 2002). It achieves particular prominence in mammals, and stimulating it electrically in conscious humans evokes powerful emotional reactions (Heath 1975; Iacono & Nashold 1982; Nashold et al. 1969). Functionally the periaqueductal gray is continuous and reciprocally interconnected with the immediately overlying deep layers of the superior colliculus (Bittencourt et al. 2005; Cadusseau & Roger 1985; Gordon et al. 2002; Grofova et al. 1978; Harting et al. 1992, Fig. 27; Sprague et al. 1961; Wiberg 1992). Here, then, in the intermediate and deep collicular connections with hypothalamus and periaqueductal gray, lies a connective interface between the brain's basic motivational systems and the orienting machinery of the collicular analog "world."

The third member of the selection triangle enters this system through the prominent projections from the substania nigra to the intermediate collicular layers (Jiang et al. 2003; Mana & Chevalier 2001; see also sects. 3.1 & 3.2). Here the final distillate of basal ganglia action-related information is interdigitated with the latticework of histochemically defined compartements that organize the input-output relations of the intermediate colliculus (Graybiel 1978; Harting et al. 1997; Illing 1992; Illing & Graybiel 1986). It appears, in other words, that the territory extending from the dorsal surface of the midbrain to the aqueduct houses the connectivity needed to implement a three-way interface of the kind outlined in the foregoing discussion, and it is hereby proposed to do so. The elements of this scheme are sketched in Figure 4.

Such a conception fits seamlessly with the proposed role of the superior colliculus in target selection outlined in section 3.2. As noted there, the selection of a traget for action is the final event in the brain's real-time decision-making regarding "what to do next." The significance of gaze control, moreover, goes far beyond the matter of moving eyes-and-head in space. The gaze plays an organizing role in a wide range of behaviors by "leading" many forms of action, as has been shown in exquisite detail for manual reaching and manipulation (Johansson et al. 2001; see also Courjon et al. 2004; Jackson et al. 2005; Schneider &

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

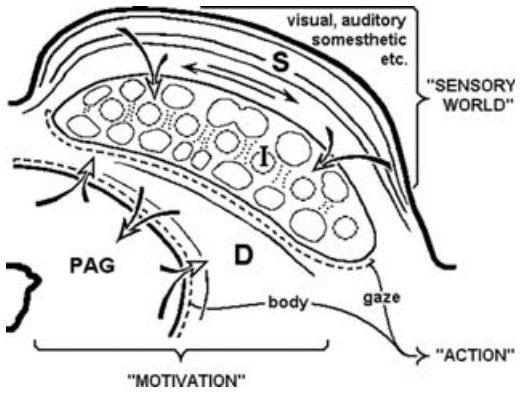


Figure 4. The three principal domains of "world" (target selection), "body" (action selection), and "motivation" (needs) that must interact to optimize decision processes in real time, portrayed in their proposed "primary" implementation in the roof of the midbrain. The extension of its logic into the forebrain, and the cerebral cortex of mammals in particular, can be conceived in terms of this primary system "writ large," as follows (cf. Fig. 6 in particular): A dorsolateral to ventromedial path from the surface of the colliculus to the midbrain aqueduct corresponds to a posterior to frontal to medial path in the cortex. In the reverse direction, and in functional terms, it reads "motivation," "action," and "world." **S**, **I**, and **D**: superficial, intermediate, and deep layers of the superior colliculus, respectively. **PAG**: the periaqueductal gray matter surrounding the midbrain cerebral aquaduct. Bidirectional arrow aligned with the collicular lamina stand for compensatory coordinate transformations. Drawing based in part on Harting et al. (1997).

Deubel 2002; Stuphorn et al. 2000; Werner et al. 1997). Nor is the output of the tecto-periaqueductal system limited to the species-specific orienting reflex: it includes escape behavior (Dean et al. 1989; Merker 1980; Sprague et al. 1961) as well as a number of innate postural schematisms associated with behaviors under periaqueductal control (Holstege et al. 1996; Lonstein et al. 1998).

In its primitive beginnings, the "world" of the proposed neural reality simulator presumably amounted to no more than a two-dimensional screen-like map of spatial directions on which potential targets might appear as mere loci of motion in an otherwise featureless noise field, defined more by their displacement than by any object features (see Stoerig & Barth 2001, for a plausible simulation). Advances on this primitive arrangement apparently proceeded by adding to it more sophisticated information from a rostral direction. Thus, the ability of a frog to side-step stationary barriers during prey-catching is dependent upon input to the tectum from the region of the caudal thalamus and pretectum, just anterior to the tectum (Ewert 1968; Ingle 1973). With the elaboration of the telencephalon, culminating in the neocortex of mammals, the arrangement was expanded further (see Section 4.5), into a fully articulated, panoramic three-dimensional world composed of shaped solid objects: the world of our familiar phenomenal experience.

4.3. Inhabiting a neural simulation

Whether primitive or advanced, the fundamental simplifying device of the proposed simulation space is to associate the origin of its shared body-world coordinate system for orienting with the head representation of its analog body. This does *not* mean that the coordinate system itself is head centered (i.e., moves with the head). At brainstem levels it appears, rather, to be oculocentric (Klier et al. 2001; Moschovakis 1996; Moschovakis & Highstein 1994). It means only that the coordinate system origin is lodged in the head representation of the simulated analog *visual* body, say in close proximity to its analog eye region. With such a location, a number of sensory-sensory mismatches and the contamination of sensory information by movement caused by the largely rotary displacements of eyes and head involved in perpetual orienting movements can be remedied – to a first approximation – by spherical coordinate transformations. This economy of control helps explain the fact that at the brainstem level not only eye movements, but also head movements, despite their very different musculo-skeletal demands, utilize a common intermediate control system organized in separate horizontal and vertical, that is, spherical, coordinates (Grobstein 1989; Masino 1992; Masino & Grobstein 1989; Masino & Knudsen 1990; see also Isa & Sasaki 2002). In humans, covert orienting of attention, as well as the visuomotor map for reaching (Gawryszewski et al. 2005; Vetter et al. 1999), appear to be framed in spherical coordinates,[3] perhaps reflecting collicular involvement in both functions (Müller et al. 2004; Werner et al. 1997).

There is reason to believe that the implicit "ego-center" origin of this coordinate space is the position we ourselves occupy when we are conscious, and that the analog body and analog world of that space is what we experience as and call our tangible, concrete body and the external world (cf. Note 2). This would explain the irreducible asymmetry adhering to the relation between perceiving subject and apprehended objects defining the conscious state. The ego-center places the conscious subject in an inherently "perspectival," viewpoint-based, relation to the contents of sensory consciousness. It is from there that objects are apprehended; objects do not apprehend the subject (cf. Merker 1997). By the same token, the one necessary constituent of consciousness that can never be an object of consciousness is that very vantage point itself, namely, the origin of the coordinate system of the simulation space. It cannot be an object of consciousness any more than an eye can see itself (Schopenhauer 1819, vol. 2, p. 491; see Baars 1988, pp. 327ff for this and other "contextual" aspects of consciousness).

Should these reasons appear somewhat abstract and rarefied, there is a far more concrete indication to the same effect. Our very body bears a tell-tale sign allowing us to recognize it as the product of a neural simulation. Vision differs topologically from somesthesis and audition by its limited angular subtense, particularly in animals with frontally directed eyes. The other two senses can be mapped *in toto* onto a spherical coordinate system for orienting, whereas vision is only partially mapped in this way. This is not in itself a problem, but becomes one given that vision can be directed, not only to the external world, but to the body itself. This necessitates some kind of junction or transition between the distal visual world and the proximal visual body, and there a problem does arise.

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Though, as we have seen, the ego-center is present in consciousness by implication only, its location can be determined empirically (Cox 1999; Hering 1879/1942; Howard & Templeton 1966; Neelon et al. 2004; Roelofs 1959). It is single, and located behind the bridge of the nose inside our head. From there we *appear* to confront the visible world directly through an empty and single cyclopean aperture in the front of our head (Hering 1879/1942; Julesz 1971). Yet that is obviously a mere appearance, since if we were literally and actually located inside our heads we ought to see, not the world, but the anatomical tissues inside the front of our skulls when looking. The cyclopean aperture is a convenient neural fiction through which the distal visual world is "inserted" through a missing part of the proximal visual body, which is "without head" as it were or, more precisely, missing its upper face region (see Harding 1961). Somesthesis by contrast maintains unbroken continuity across this region. The empty opening through which we gaze out at the world betrays the simulated nature of the body and world that are given to us in consciousness. The essentials of the arrangement are depicted in highly schematic form in Figure 5.

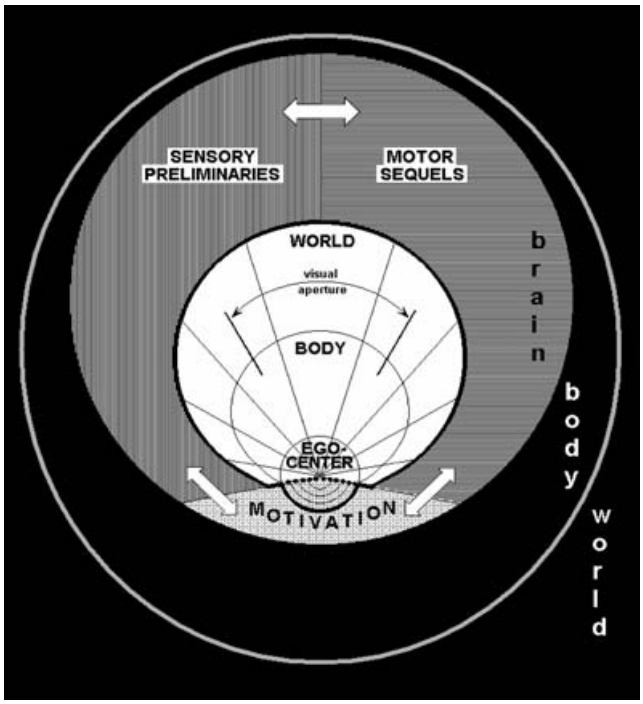


Figure 5. Highly schematic depiction of the nested relation between ego-center, neural body, and neural world constituting the analog neural simulation ("reality space") proposed as a solution to the tri-partite selection problem described in the text. Black depicts the physical universe, one part of which is the physical body (black oval), both of which are necessarily outside of consciousness. One part of the physical body is the physical brain (circle; shaded and unshaded). It contains the "reality space" of consciousness (unshaded), separated from other, nonconscious (shaded) functional domains by a heavy black line, signifying their exclusion from consciousness. Arrows mark interfaces across which neural information may pass without entering consciousness. The designation ego-center is a sensorimotor construct unrelated to the concept of self-consciousness. See text for further details.

The simulated nature of our body and world is further supported by a number of phenomena that alert us to the synthetic nature of what we typically take to be physical reality itself, that is, phenomena such as inattention blindness, change blindness, and allied effects (O'Reagan et al. 2000; Rensink 2002; Rensink et al. 1997; Simons & Chabris 1999). Such "deletions from consciousness" can be countered by appropriately placed microstimulation of the superior colliculus (Cavanaugh & Wurtz 2004; see also Müller et al. 2005). These various indications all support the conclusion that what we confront in sensory consciousness is indeed a simulated (synthetic) world and body.

As central residents of that simulation, we are subject to ever shifting moods, feelings, urges, emotions, and impulses. These, then, would be those aspects of the brain's motivational dynamics that reach consciousness (cf. Cabanac 1992; Panksepp 1982; 1998a). The reason they do so, according to the present proposal, is their relevance to the tripartite determination of what to do next, as outlined in the foregoing discussion. A striking illustration of this principle is afforded by respiratory control (Merker 2005). It is automatic and unconscious as long as partial pressures of blood gases stay within normal bounds, yet intrudes most forcefully on consciousness in the form of an acute sense of panic when they go out of bounds. Extreme blood gas values are an indication that urgent action on the environment – such as removing an airway obstruction or getting out of a carbon dioxide filled pit – may be imperative. That is what suddenly makes action selection and target selection relevant to respiratory control, which accordingly "enters consciousness" in the form of a powerful feeling of suffocation.

This example further illustrates the lack of any necessary connection between cognitive sophistication and the reason for something to enter consciousness. Even quite elementary functions may benefit from the efficiency provided by the triangular action-target-motivation interface of consciousness. It serves optimal decision-making in real time, on the broad front of its tripartite information base, concisely packaged in its multivariate simulation space. Such a utility is particularly valuable when a moment's hesitation may make a big difference in outcome, as in the suffocation example (but also in, say, agonistic encounters), quite apart from anything to do with advanced cognition. The evolution of such a utility could accordingly proceed independently of cognitive capacity, to crown the optic brain with its tectal machinery at the very outset of the vertebrate lineage.

In its peculiar nesting of a body inside a world, around an ego-center in a shared coordinate space subject to motivational bias, this interface possesses the essential attributes of phenomenal consciousness. As implemented in the midbrain and diencephalon, the arrangement is proposed to have served as the innate scaffolding supporting all further elaboration of conscious contents in phylogeny. Centered on the colliculus extending into periaqueductal gray, it will be further defined in section 4.5. A felicitous term for the functional state supported by the basic (mesodiencephalic) arrangement would accordingly be "primary consciousness" (Hodgson 1878; Petty 1998; Trevarthen & Reddy 2006).

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

4.4. Coherent, motivated behavior under sensory guidance in the absence of the cerebral cortex

The superordinate functional position attributed to mesodiencephalic mechanisms in previous sections of this article is supported by a number of empirical findings that receive a unified interpretation in this light. When the behavioral effects of local brain stimulation are systematically surveyed by means of depth electrodes, it is common to find that the most coherent, integrated, and natural-looking (whole, or "molar") behavioral reactions – be they orienting, exploration, or a variety of appetitive, consummatory, and defensive behaviors – are evoked by stimulation of diencephalic and midbrain sites, whereas stimulation at more rostral or caudal levels tends to evoke more fragmentary or incomplete behaviors (Adams 1979; Bandler & Keay 1996; Bard 1928; Brandao et al. 1999; Carrive et al. 1989; Fernandez de Molina & Hunsperger 1962; Hess 1954; Hess & Brugger 1943; Holstege & Georgiadis 2004; Hunsperger 1956; 1963; Hunsperger & Bucher 1967; Kaada 1951; Orlovsky & Shik 1976; Schaefer & Schneider 1968; Schuller & Radtke-Schuller 1990).

All of the behaviors just mentioned have also been exhibited by experimental animals after their cerebral cortex has been removed surgically, either in adulthood or neonatally. Best studied in this regard are rodents (Whishaw 1990; Woods 1964). After recovery, decorticate rats show no gross abnormalities in behavior that would allow a casual observer to identify them as impaired in an ordinary captive housing situation, although an experienced observer would be able to do so on the basis of cues in posture, movement, and appearance (Whishaw 1990; what follows relies on Whishaw's study, supplemented by additional sources as indicated). They stand, rear, climb, hang from bars, and sleep with normal postures (Vanderwolf et al. 1978). They groom, play (Panksepp et al. 1994; Pellis et al. 1992), swim, eat, and defend themselves (Vanderwolf et al. 1978) in ways that differ in some details from those of intact animals, but not in outline. Either sex is capable of mating successfully when paired with normal cage mates (Carter et al. 1982; Whishaw & Kolb 1985), though some behavioral components of normal mating are missing and some are abnormally executed. Neonatally decorticated rats as adults show the essentials of maternal behavior, which, though deficient in some respects, allows them to raise pups to maturity. Some, but not all, aspects of skilled movements survive decortication (Whishaw & Kolb 1988), and decorticate rats perform as readily as controls on a number of learning tests (Oakley 1983). Much of what is observed in rats (including mating and maternal behavior) is also true of cats with cortical removal in infancy: they move purposefully, orient themselves to their surroundings by vision and touch (as do the rodents), and are capable of solving a visual discrimination task in a T-maze (Bjursten et al. 1976; see also Bard & Rioch 1937).

The fact that coherent and well-organized molar behaviors are elicited by local stimulation in the mesodiencephalic region of intact animals and that coherent motivated behavior under environmental guidance is displayed spontaneously by animals lacking a cerebral cortex means that the neural mechanisms required to motivate, orchestrate, and provide spatial guidance for these behaviors are present in the parts of the brain that remain after decortication. Some aspects of these behaviors are dependent upon basal ganglia and basal forebrain functions remaining after the loss of their principal (cortical) source of afference (Wishaw 1990, p. 246), whereas the basic competences of decorticate animals reflect the capacity of upper brainstem mechanisms to sustain the global patterning, emotional valence, and spatial guidance of the postures and movements of orienting, defense, aggression, play, and other appetitive and consummatory behaviors (Adams 1979; Holstege & Georgiadis 2004; Masino 1992; Maskos et al. 2005; Panksepp 1982; Sakuma & Pfaff 1979; Swanson 2000). The particulars of the dependence of these behaviors on key structures located in the mesodiencephalic region has been repeatedly reviewed (Bassett & Taube 2001; Behbehani 1995; Groenewegen 2003; Haber & Fudge 1997; Horvitz 2000; Houk 1991; Jurgens 1994; Mouton 1999; Padel 1993; Panksepp 1998a; Prescott et al. 1999; Swanson 1987; 2000; ten Donkelaar 1988; Watt 2000; Watt & Pincus 2004; Winn 1998; Zahm 2006).

It is into the premotor circuitry of these ancient and highly conserved upper brainstem mechanisms that a wide range of systems place their bids for "where to look" and "what to do," irrespective of the level of sophistication of any one of these "bidding" systems. Each of them has independent access to effectors, and their upper brainstem interactions are not infrequently mediated by collaterals of such projections. The cerebral cortex is one prominent input to this system through the direct and indirect fiber projections emphasized in the foregoing discussion and sketched in Figure 3 (see also Swanson 2000). This relationship is, however, not a one-way affair. In fact, the manner in which the telencephalon is interfaced and integrated with the mesodiencephalic control system adds further definition to the central role of upper brainstem mechanisms in conscious functions.

4.5. Including the forebrain

Three cortical regions figure repeatedly and prominently in studies of cerebral mechanisms related to attention, neglect, and consciousness: namely, the posterior parietal cortex, the prefrontal cortex, and a medial territory centered on the cingulate gyrus (Baars et al. 2003, Fig. 1; Blumenfeld & Taylor 2003; Clower et al. 2001; Corbetta 1998; Han et al. 2003; Lynch et al. 1994; Mesulam 1999; Posner & Petersen 1990; Raz & Buhle 2006; Rees & Lavie 2001). A special connective and functional relationship exists between these three cortical territories and the mesodiencephalic system outlined in the foregoing discussion. It is most easily approached by considering their mutual interface in the nuclei of the dorsal thalamus. The latter can be divided into first-order (largely sensory relay) and higher-order ("association") thalamic nuclei (Sherman & Guillery 2001), and it is with the latter, *higher-order* nuclei, that the mesodiencephalic system maintains an intimate and complex relationship.

The two major higher-order nuclei of mammals are the mediodorsal nucleus, whose cortical projections define the prefrontal cortex, and the pulvinar complex related to a set of posterior cortical areas, including extrastriate visual

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

areas such as those of the posterior parietal cortex. Though proposed to serve as thalamic relays for cortico-cortical interactions (Sherman & Guillery 2001), these nuclei are not devoid of extra-telencephalic input, and both receive prominent input from the superior colliculus (Benevento & Fallon 1975; Harting et al. 1980; Lyon et al. 2005). Afferents to the pulvinar originate largely from the superficial collicular layers, whereas those destined for the mediodorsal nucleus are predominantly of intermediate layer origin. The latter projection targets a zone at the lateral edge of the mediodorsal nucleus related to the frontal eye fields (see Sommer & Wurtz 2004), the cortical territory most directly implicated in unilateral neglect of frontal origin (see Mesulam 1999, and references therein).

The cingulate gyrus, finally, is related to the mesodiencephalic system by its projections to the intermediate and deep layers of the colliculus (Harting et al. 1992; Sherman et al. 1979), the periaqueductal gray matter (An et al. 1998; Floyd et al. 2000), and by a conspicuously heavy projection to the *zona incerta* (Mitrofanis & Mikuletic 1999, Figs. 6 and 7). This latter structure is a mammalian derivative of the ventral thalamus of comparative terminology mentioned in section 4.1, and has emerged from obscurity only recently (see review by Mitrofanis 2005). It sends a topographically organized inhibitory projection to the superior colliculus, and reaches up into the thalamus above it to selectively innervate its higher-order nuclei bilaterally, likewise with powerful GABAergic inhibition (Barthó et al. 2002; Lavallée et al. 2005; Power et al. 1999; Trageser & Keller 2004).

Collicular input to the higher-order nuclei is excitatory, whereas their incertal input is inhibitory. This implies dynamic competition between colliculus and zona incerta for influence over the two principal thalamic dependencies of the prefrontal and the posterior parietal cortex. In this competition the inhibitory incertal element stands under cingulate cortex influence and is also in a position to inhibit the colliculus directly and with topographic specificity (Ficalora & Mize 1989; Kim et al. 1992; Ma 1996; May et al. 1997). These circumstances cannot but profoundly affect the functional dynamics of the three cortical territories with which we are concerned. The principal pathways relating them to the mesodiencephalic control system and the higher-order thalamic nuclei are depicted schematically in Figure 6.

Supplying a key node in the relations depicted in Figure 6, the zona incerta is monosynaptically (and often reciprocally and bilaterally) connected with on the order of 50 separate structures along the entire length of the neuraxis from spinal cord to olfactory bulb (my own conservative inventory of the literature, not counting connections with individual cortical areas separately). Internally, the zona incerta features profuse mutual connectivity in a setting of cytoarchitectonic and cytological heterogeneity in which GABAergic cells are prominent (Benson et al. 1991; 1992; Nicolelis et al. 1992; see Power & Mitrofanis 1999; 2001; and Bartho et al. 2002, p. 1002, for connective details). A combination of reciprocal external connectivity with internal mutual inhibition is the theoretically optimal solution for implementing global competitive interaction among structures separated by long distances (for background, see McFarland 1965; Snaith & Holland 1990; Prescott et al. 1999, pp. 27–29). The zona incerta accordingly may implement such a scheme, and is hereby proposed to do so, as schematically illustrated in Figure 7.

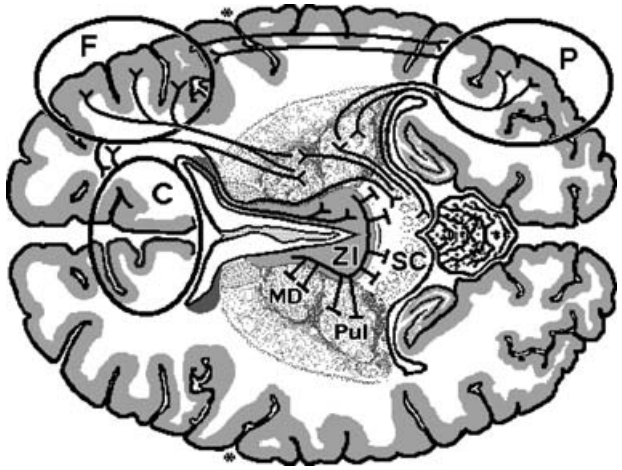


Figure 6. Composite diagram illustrating the interface between the mesodiencephalic system and the thalamocortical complex. Principal pathways by which the superior colliculus and the zona incerta relate to one another, as well as to the dorsal thalamus and the cerebral cortex, are indicated in black heavy lines. Excitatory connections end in a "Y", inhibitory connections in a "T". Abbreviations: **P**: parietal; **F**: frontal; **C**: cingulate cortex; **SC**: superior colliculus; **ZI**: zona incerta; **Pul**: pulvinar complex; **MD**: mediodorsal nucleus of the thalamus. The central sulcus is marked by an asterisk. See text for further detail.

The zona incerta – or the ventral thalamus of non-mammals – thus supplies the integrative machinery of the optic brain with a connective hub that seems designed to conduct mutually inhibitory trials of strength among a truly diverse set of afferents. They include, but are not limited to, visual, auditory, somatosensory, vestibular (Horowitz et al. 2005), cerebellar, striatal, collicular, motor, and limbic ones. The outcome of the competition – a neural decision – is conveyed to the intermediate and deep layers of the superior colliculus by a topographically organized inhibitory projection, as already mentioned. The collicular return projection to the zona incerta – like that of many incertal afferents – is non-topographic, implying greater specificity of incertal influence over the colliculus than the reverse. At the same time, incertal inhibitory output ascends into the association nuclei of the dorsal thalamus, establishing the zona incerta as a connective bridge straddling the mesodiencephalic and the thalamocortical systems.

Coupled with the scope of its connectivity along the neuraxis, this nodal position of the zona incerta lends it a potentially strategic role as an arbiter of moment-to-moment decision-making "in the light of all available evidence." As in the case of collicular target selection, the loss of such a high-level function need not generate conspicuous behavioral deficits, and does not appear to do so in rats with incertal lesions (Thompson & Bachman 1979). Rather, it would be expected to issue in suboptimal levels of resource allocation relative to shifting patterns of multiply interacting opportunities and needs. Preliminary indications regarding the great diversity and complexity of neuronal response properties in the zona incerta are worthy of note in this connection (Crutcher

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

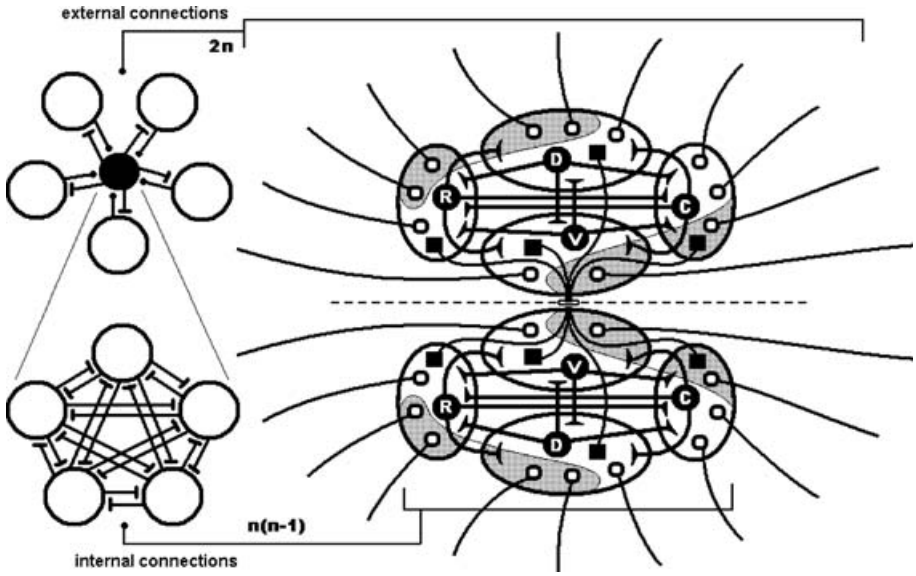


Figure 7. Schematic diagram illustrating zona incerta connectivity to the rest of the brain and of its subdivisions to one another, depicted bilaterally to emphasize the prominent commissural, "midline-straddling," nature of incertal connectivity. Ovals represent the principal incertal subnuclei, shown physically separated for graphical clarity. Labels **R**, **D**, **V**, and **C** mark the rostral, dorsal, ventral, and caudal subnuclei, respectively, and connections among them. Filled squares indicate that each subnucleus projects to all subnuclei on the opposite side. Open circles stand for incertal connections with the rest of the brain (typically reciprocal in nature). Shaded regions stand symbolically for the fact that functionally defined subregions of the zona incerta (sensory modalities, motor, limbic, etc.) often cut across its nuclear subdivisions. Inserts on the left summarize the two connective schemes that appear to be combined in the zona incerta. Long-distance (external) connections, for which wiring-efficiency is at a premium, connect n entities to a central hub (the zona incerta itself) by 2n (i.e., reciprocal) connections (expandable to new targets at the low cost of 2). Internal connectivity within the zona incerta (wiring efficiency *not* at a premium), by contrast, appears to follow the n(n – 1) connective principle (lower diagram, expanding the filled central circle of the upper diagram). The scheme as a whole idealizes evidence supplied by the pioneering studies of Mitrofanis and colleagues (references in the text), and awaits refinement in the light of further detailed studies.

et al. 1980; Kendrick et al. 1991; Ma 1996; Mungarndee et al. 2002; Nicolelis et al. 1992).

Finally, the zona incerta lies in immediate anterior continuity with the prerubral field and rostral interstitial nucleus of the medial longitudinal fasciculus, that is, with the rostral-most pole of the intermediate control system for orienting organized in spherical coordinates, mentioned in section 4.3. This rostral pole is specialized for vertical movement, whereas the system's horizontal components are found farther caudally, in paramedian reticular structures extending into the pons. Could it be that the zona incerta supplies a kind of origin for this coordinate system, a midline-straddling point of unity connected directly and via the colliculus to the rest of the coordinate space (Giolli et al. 2001; Kolmac et al. 1998; Leichnetz et al. 1987)? Incertal omnipause neurons are at least compatible with such an eventuality (Hikosaka & Wurtz 1983; Ma 1996). Nothing would be more elegant than to entrust the final arbitration of "what to do next" to a self-inhibitory "winner-take-all" or other decision network (Richards et al. 2006) lodged at the origin of the coordinate system that controls the orienting movements which execute that decision once made. As a primary perspectival viewpoint charged with changing motives, it would possess the essential attributes of a self (see sect. 4.3). Prominent incertal afference from cingulate cortex would fit such a role (cf. Northoff et al. 2006 for medial cortex and self), but short of further evidence, the suggestion must remain speculative.

4.5.1. Collicular gamma oscillations and cortical "binding.". The superior colliculus is the only place outside of the cerebral cortex in which fast oscillations in the gamma range have been shown to occur and to behave in a manner paralleling in all significant respects that of the cortex (Brecht et al. 1998; 1999; 2001). At the cortical level such oscillatory activity has been proposed to serve a "binding" function for consciousness (in the sense of integrating disparate elements of unitary conscious percepts) on circumstantial grounds (Engel et al. 1999; Engel & Singer 2001; Singer 2001). As we shall see, one need not, however, ascribe a unique role to gamma oscillations in either binding or consciousness to recognize that they may have consequences for cortico-collicular integration nevertheless.

Though sometimes portrayed as "the" problem of consciousness, the acuteness of the cortical binding problem must not be exaggerated. The pyramid architecture of point-to-point interareal connectivity within topographically organized cortical sensory domains ensures that corresponding points on areal topographies featuring different functional content (e.g., contour and color) are *connectively* and thus coherently related, even though the areas themselves occupy separate locations in the cortical sheet (Felleman & VanEssen 1991; cf. Fig. 2 and Note 2 of Merker 2004a).

The laminar superposition of numerous cortical areas in the colliculus takes this principle further. Here the joining of corresponding points on different cortical maps takes

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

place by direct laminar superposition of topographic projections of different cortical areas within a unified collicular topography. Thus, the output of different cortical areas are brought within the compass of the dendritic trees of single collicular neurons, which often straddle collicular laminar boundaries (Albers & Meek 1991; Laemle 1983; Langer & Lund 1974; Ma et al. 1990). Tight temporal synchrony of neuronal firing in separate cortical loci (through coupling to gamma oscillations) increases the probability that their joint activity will fall within the temporal window of integration of any neuron – whether cortical or subcortical – to which they project convergently (Abeles 1982; König et al. 1996). Synchronous activation of corresponding loci on separate cortical maps would accordingly assist such activity in crossing collicular thresholds by summation via the dendritic trees of convergently innervated collicular cells.

In crossing the collicular threshold – whether assisted by gamma synchrony or not – cortical activity would gain access to the mesodiencephalic system in all of its ramifications, projections to the cortex included (see Fig. 6). This, according to the present account, would be a principal step by which such activity enters awareness. If so, it follows that *one conscious content will not be replaced by another without involvement of the mesodiencephalic system (centered on the superior colliculus) as outlined here, even when that change is unaccompanied by eye movements.* This prediction is specific to the present perspective, and accordingly renders it testable. The means for doing so are exemplified by a recent functional imaging study of a visual-auditory illusion in humans (Watkins et al. 2006). That study revealed collicular activation associated with awareness of the illusion, though stimuli were identical on trials in which the illusion was not perceived, and central fixation was maintained throughout, confirming the prediction just made, in this particular instance.

This, then, would be the identity of the so far unidentified threshold featured in a recent programmatic proposal regarding conscious function (Crick & Koch 2003). Its identification with the threshold for access to the mesodiencephalic system centered on the colliculus (Figs. 4 & 6) is reinforced by the fact that layer V pyramidal cells supply the sole cortical projection to the colliculus. These cells exhibit a number of notable specializations: they do *not* give off collaterals to the thalamic reticular nucleus on passing through it (Jones 2002), their local intra-cortical connectivity appears stereotyped (Kozloski et al. 2001), and their apical dendrites branch in cortical layer I and carry specialized conductance mechanisms activated by top-down (feedback) connections in the superficial cortical layers (Larkum et al. 2004). This may ensure that activation of both the feedforward and feedback cortical system is typically required for the corticomesencephalic threshold to be crossed, such concurrent activation having been proposed as an essential condition for cortical information to reach awareness (Lamme & Spekreijse 2000; see also Merker 2004a, p. 566).

4.5.2. Consciousness and cortical memory. Penfield and Jasper proposed a role for the centrencephalic system in both consciousness and the laying down of cortical memories across the life span. A rationale for such a memory role is suggested by the present perspective. The perpetual and cumulative nature of cortical memory recording (Merker 2004a; 2004b; Standing 1973) puts a premium on economy of storage, that is, on concentrating memory recording to significant information (Haft 1998). A criterion for doing so is available in the system of integration for action as outlined here: Information that is important enough to capture control of behavior (i.e., by triggering an orienting movement placing its target in focal awareness) is also important enough to be consigned to permanent cortical storage. The focal presence of the target obviously will be the greater part of ensuring such an outcome, but it is likely to be actively supported as well by the system of dual colliculo-thalamic relays to cortex (cf. Fig. 6). From its parietal and frontal target areas, accessed in part via so-called matrix cell projections from the thalamus to the superficial cortical layers (Jones 1998), the mesodiencephalic influence would then propagate and spread through the cortex via intracortical top-down feedback connectivity.

The evidence for a "general learning system" (which includes the superior colliculus: Thompson 1993), mentioned in the introduction to section 3, would seem to bear on this proposal, as well. In fact, the severe capacity limitations of so called working memory (Baddeley 1992; Cowan 2001; Mandler 1975) are likely to derive in large part from the mesodiencephalic bottleneck which all attended (i.e., conscious) information must access according to the present proposal, just at the point where the parallel distributed data format of the forebrain *requires* conversion to a serial, limited capacity format to serve behavior.

4.5.3. The zona incerta and the seizures of absence epilepsy. It is to be noted, finally, that the Penfield and Jasper postulation of a centrencephalic system *symmetrically related to both cerebral hemispheres* was motivated in part by observations on the generalized seizures of absence epilepsy. The zona incerta sends a rich complement of commissural fibers across the midline not only to itself, but also to the association nuclei of the dorsal thalamus (Power & Mitrofanis 1999; 2001). It is also a prime locus for the induction of generalized epileptic seizures, being more sensitive than any other brain site to their induction by local infusion of carbachol (Brudzynski et al. 1995; see also Gioanni et al. 1991; Hamani et al. 1994). A number of phenomena that may accompany absence seizures can be readily related to the zona incerta. Thus, a forward bending or dropping of the head (or bending of the whole body to the ground; Penfield & Jasper 1954, p. 28) may relate to the already mentioned fact that the transition between the zona incerta and midbrain contains mechanisms for vertical control of eyes and head (Holstege & Cowie 1989; Waitzman et al. 2000; cf. sect. 4.2). The fluttering of the eyelids that often occurs in the same situation is also easily accommodated by the functional anatomy of this region (Morcuende et al. 2002; Schmidtke & Buttner-Ennever 1992).

The Penfield and Jasper definition of their proposed centrencephalic system always included explicit reference to the midbrain reticular formation. The zona incerta resembles a forward extension of the midbrain reticular formation beneath the thalamus (Ramón-Moliner & Nauta 1966), and much of the functional anatomy of the diencephalon needs to be re-examined in light of its

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

unusual connectivity. As noted by Barthó et al. (2002), the identification of a second, incertal, source of GABAergic innervation of the dorsal thalamus, in addition to that of the thalamic reticular nucleus, necessitates a re-evaluation of the entire issue of the nature of thalamic involvement in seizure generation and oscillatory thalamocortical activity (McCormick & Contreras 2001; Steriade 2001). This is all the more so since the even more recent discovery of a third source of powerful GABAergic thalamic inhibition, originating in the anterior pretectal nucleus (Bokor et al. 2005). One need not, however, await the outcome of such re-examination to identify the zona incerta as the perfect anatomical center-piece for the Penfield and Jasper centrencephalic hypothesis, though its obscurity at the time kept it from being recognized as such.

5. Consciousness in children born without cortex

Anencephaly is the medical term for a condition in which the cerebral hemispheres either fail to develop for genetic-developmental reasons or are massively compromized by trauma of a physical, vascular, toxic, hypoxic-ischemic, or infectious nature at some stage of their development. Strictly speaking, the term is a misnomer. The brain consists of far more than cerebral hemispheres or prosencephalon, yet various conditions of radical hemispheric damage are historically labelled anencephaly. When the condition is acquired, for example, by an intrauterine vascular accident (stroke) of the fetal brain, the damaged forebrain tissue may undergo wholesale resorption. It is replaced by cerebrospinal fluid filling otherwise empty meninges lining a normally shaped skull, as illustrated in Figure 8. The condition is then called hydranencephaly (Friede 1989), and is unrelated to the far more benign condition called hydrocephalus, in which cortical tissue is compressed by enlarging ventricles but is present in anatomically distorted form (Sutton et al. 1980).

The loss of cortex must be massive to be designated hydranencephaly, but it is seldom complete (see Fig. 8). It typically corresponds to the vast but somewhat variable forebrain expanse supplied by the anterior cerebral circulation (Myers 1989; Wintour et al. 1996). Variable remnants of cortex supplied by the posterior circulation, notably inferomedial occipital, but also basal portions of temporal cortex, and midline cortical tissue along the falx extending into medial frontal cortex, may be spared. The physical presence of such cortical tissue, clearly visible in Figure 8, need not mean, however, that it is connected to the thalamus (white matter loss often interrupts the visual radiations, for instance) or that it is even locally functional. On autopsy, such tissue may be found to be gliotic on microscopic examination or to exhibit other structural anomalies indicating loss of function (Marin-Padilla 1997; Takada et al. 1989). As Figure 8 shows, most cortical areas are simply missing in hydranencephaly, and with them the organized system of cortico-cortical connections that underlie the integrative activity of cortex and its proposed role in functions such as consciousness (Baars et al. 2003; Sporns et al. 2000).

An infant born with hydranencephaly may initially present no conspicuous symptoms (Andre et al. 1975), and occasionally the condition is not diagnosed until several months postnatally, when developmental milestones are missed. In the course of the first year of life, which is often though not invariably difficult, these infants typically develop a variety of complications that always include motoric ones (tonus, spasticity, cerebral palsy), and often include seizures, problems with temperature regulation, reflux/aspiration with pulmonary sequelae, and other health problems occasioning medical emergencies and attended by a high mortality rate. Were

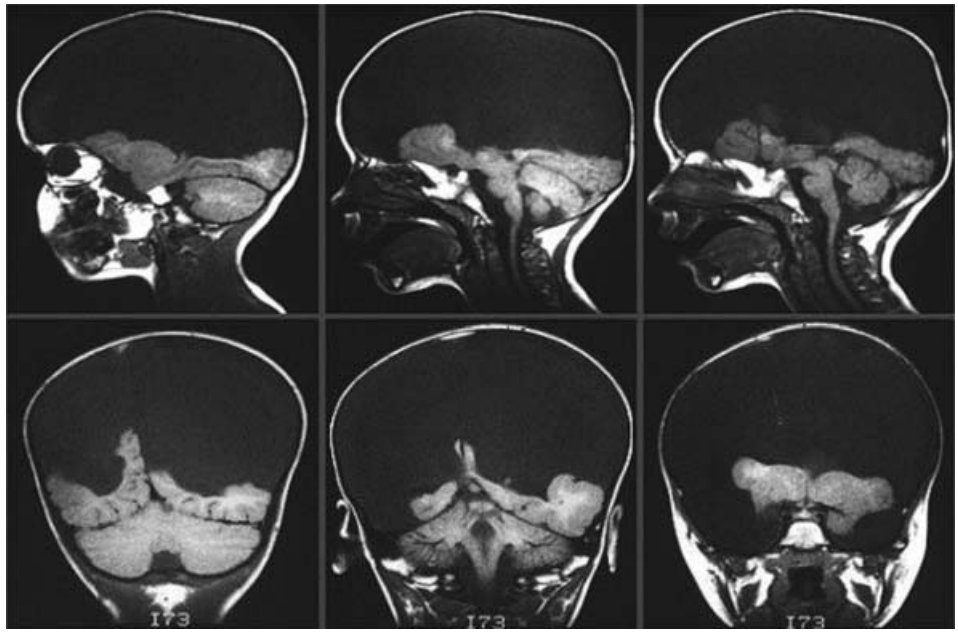


Figure 8. Saggittal and frontal magnetic resonance images of the head of a child with hydranencephaly. Spared ventromedial occipital and some midline cortical matter overlies an intact cerebellum and brainstem, whereas the rest of the cranium is filled with cerebrospinal fluid. Reprinted with the kind permission of the American College of Radiology (ACR Learning File, Neuroradiology, Edition 2, 2004).

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

one to confine one's assessment of the capacities of children with hydranencephaly to their presentation at this time – which for natural reasons is the period in the lives of these children to which the medical profession has the most exposure – it would be all too easy to paint a dismal picture of incapacity and unresponsiveness as the hydranencephaly norm. When, however, the health problems are brought under control by medication and other suitable interventions such as shunting to relieve intracranial pressure, the child tends to stabilize and with proper care and stimulation can survive for years and even decades (Counter 2005; Covington et al. 2003; Hoffman & Liss 1969; McAbee et al. 2000).

When examined after such stabilization has taken place, and in the setting of the home environment upon which these medically fragile children are crucially dependent, they give proof of being not only awake, but of the kind of responsiveness to their surroundings that qualifies as conscious by the criteria of ordinary neurological examination (Shewmon et al. 1999). The report by Shewmon and colleagues is the only published account based upon an assessment of the capacities of children with hydranencephaly under near optimal conditions, and the authors found that each of the four children they assessed was conscious. For detail, the reader is referred to the case reports included in the Shewmon et al. (1999) publication. Anecdotal reports by medical professionals to the same effect occasionally see print (Counter 2005), but compared to its theoretical and medical importance the issue remains woefully underexplored.

To supplement the limited information available in the medical literature on the behavior of children with hydranencephaly, I joined a worldwide internet self-help group formed by parents and primary caregivers of such children. Since February of 2003 I have read more than 26,000 e-mail messages passing between group members. Of these I have saved some 1,200 messages containing informative observations or revealing incidents involving the children. In October 2004 I joined five of these families for one week as part of a social get-together featuring extended visits to DisneyWorld with the children, who ranged in age from 10 months to 5 years. I followed and observed their behavior in the course of the many private and public events of that week, and documented it with four hours of video recordings.

My impression from this first-hand exposure to children with hydranencephaly confirms the account given by Shewmon and colleagues. These children are not only awake and often alert, but show responsiveness to their surroundings in the form of emotional or orienting reactions to environmental events (see Fig. 9 for an illustration), most readily to sounds, but also to salient visual stimuli (optic nerve status varies widely in hydranencephaly, discussed further on). They express pleasure by smiling and laughter, and aversion by "fussing," arching of the back and crying (in many gradations), their faces being animated by these emotional states. A familiar adult can employ this responsiveness to build up play sequences predictably progressing from smiling, through giggling, to laughter and great excitement on the part of the child. The children respond differentially to the voice and initiatives of familiars, and show preferences for certain situations and stimuli over others, such as a specific familiar toy, tune, or video program, and



Figure 9. The reaction of a three-year-old girl with hydranencephaly in a social situation in which her baby brother has been placed in her arms by her parents, who face her attentively and help support the baby while photographing.

apparently can even come to expect their regular presence in the course of recurrent daily routines.

Though behavior varies from child to child and over time in all these respects, some of these children may even take behavioral initiatives within the severe limitations of their motor disabilities, in the form of instrumental behaviors such as making noise by kicking trinkets hanging in a special frame constructed for the purpose ("little room"), or activating favorite toys by switches, presumably based upon associative learning of the connection between actions and their effects. Such behaviors are accompanied by situationally appropriate signs of pleasure or excitement on the part of the child, indicating that they involve the kind of coherent interaction between environmental stimuli, motivational-emotional mechanisms, and bodily actions for which the mesodiencephalic system outlined in this article is proposed to have evolved. The children are, moreover, subject to the seizures of absence epilepsy. Parents recognize these lapses of accessibility in their children, commenting on them in terms such as "she is off talking with the angels," and parents have no trouble recognizing when their child "is back." As discussed earlier, episodes of absence in this form of epilepsy represent a basic affliction of consciousness (cf. Blumenfeld & Taylor 2003). The fact that these children exhibit such episodes would seem to be a weighty piece of evidence regarding their conscious status.

In view of the functional considerations reviewed in the foregoing, none of these behavioral manifestations in children with hydranencephaly ought to occasion any surprise, and no special explanations such as neural reorganization based on plasticity are needed to account for them. Rather, they are what the nodal position of mesodiencephalic mechanisms in convergent neural integration, along with the comparative evidence regarding the behavior of mammals in the absence of cerebral cortex, would lead us to expect. Nor is there much warrant for attempting to attribute these behaviors to remnant cortical tissue. Besides the questionable functional status of spared cortex already alluded to, a significant functional asymmetry speaks directly against it. As common as it is for some occipital cortex to remain in these individuals, so is it rare for any auditory cortex to be spared. Yet, sensory responsiveness in hydranencephaly shows the opposite asymmetry: hearing is generally preserved, whereas vision tends to be compromised (Hydranencephaly Group Survey 2003). The pattern is easily accounted for by the intactness of the

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

brainstem auditory system in these children (Lott et al. 1986; Yuge & Kaga 1998), crowned by a projection from inferior to superior colliculus. By contrast, vision in these children is liable to be compromised already at the level of the optic nerve. The latter's blood supply through the anterior cerebral circulation exposes it to damage in hydranencephaly, and its status varies widely in affected children (Jones & France 1978).

What is surprising, instead, is the routine classification of children with hydranencephaly into the diagnostic category of "vegetative state" (Multi-Society Task Force 1994), apparently in conformity with a theoretical identification between the cortex as an anatomical entity and consciousness as a function. It is this very identification which has been under critical examination in the present target article. To the extent to which the arguments and the evidence presented here have any merit, such an identification is not tenable, and the routine attribution of a lack of awareness to children lacking cortex from birth would accordingly be inadmissible. The extent of awareness and other capacities in these children must be based on assessment in its own right, by appropriate neurological tests, and not by reference to the status of their cortical tissue (Shewmon 2004). Moreover, considering the medically fragile status of many of these children, such behavioral assessment must be performed under optimal circumstances.

Properly assessed, the behavior of children with early loss of their hemispheres opens a unique window on the functional capacities of a human brainstem deprived of its cerebral cortex early in intrauterine development. They tell us, for one thing, that the human brainstem is specifically human: these children smile and laugh in the specifically human manner, which is different from that of our closest relatives among the apes (Provine & Yong 1991; van Hooff 1972). This means that the human brainstem incorporates mechanisms implementing specifically human capacities, as shown long ago by the neurologist Gamper on the basis of his detailed cinematographically documented account of a congenitally anencephalic girl entrusted to his care (Gamper 1926). In her case, there is no possibility that remnant hemispheric tissue might account for her human smile, since detailed postmortem histology disclosed that she had no neural tissue above the level of the thalamus, and even her thalamus was not functional.

The implication of the present account is that unless there are further complications, such a child should be *expected* to be conscious, that is, possessed of the primary consciousness by which environmental sensory information is related to bodily action (such as orienting) and motivation/emotion through the brainstem system outlined in the foregoing. The basic features of that system evolved long before the cerebral hemispheres embarked on their spectacular expansion in mammals to supply it with a new form of information based upon cumulative integration of individual experience across the lifetime (see Merker 2004a). Now as then, this brainstem system performs for the cortex, as for the rest of the brain, a basic function: that of integrating the varied and widely distributed information needed to make the best choice of the very next act. That function, according to the present account, is the essential reason for our being conscious in the first place. The integrated and coherent relationship it establishes between environmental events, motivation/emotion, and actions around the pivotal node of an egocenter would seem to offer a definition of a "being" in biological terms.

6. Implications for medical ethics

Needless to say, the present account has ramifying implications for issues in medical ethics. One of these concerns pain management in children with hydranencephaly and similar conditions. It is not uncommon for parents to encounter surprise on the part of medical professionals when requesting analgesia or anesthesia for their crying child during invasive procedures, a situation in some ways reminiscent of what was found in the case of neonates only a few decades back (Anand & Hickey 1987). They also extend to more general issues pertaining to the quality of care appropriate to these children, and ultimately to questions such as the meaning of personhood and even medical definitions of death (see, e.g., Shewmon et al. 1989, and references therein). Such questions are decidedly beyond the scope of the present article, which is meant only to raise those issues of a theoretical and empirical nature which are prior to and essential for finding reasoned and responsible answers to the ethical ones. Suffice it to say that the evidence surveyed here gives no support for basing a search for such answers on the assumption that "awareness," in the primary sense of coherent relatedness of a motivated being to his or her surroundings, is an exclusively cortical function and cannot exist without it.

7. Conclusion

The evidence and functional arguments reviewed in this article are not easily reconciled with an exclusive identification of the cerebral cortex as the medium of conscious function. They even suggest that the primary function of consciousness – that of matching opportunities with needs in a central motion-stabilized body–world interface organized around an ego-center – vastly antedates the invention of neocortex by mammals, and may in fact have an implementation in the upper brainstem without it. The tacit consensus concerning the cerebral cortex as the "organ of consciousness" would thus have been reached prematurely, and may in fact be seriously in error. This has not always been so, as indicated by the review of the Penfield and Jasper (1954) "centrencephalic" theory of consciousness and volitional behavior with which we began. As we have seen, their proposal has not only been strengthened by certain findings accumulating since it was first formulated more than half a century ago, but, suitably updated, it still appears capable of providing a general framework for the integration of a vast array of diverse facts spanning from the basics of the vertebrate brain plan to evidence for awareness in children born without a cortex. Whether such a framework can be developed into a comprehensive account of the neural organization of consciousness will depend upon resolving a number of the empirical and theoretical questions left unanswered in the foregoing discussion. Preliminary though it may be, that discussion suggests that part of the endeavor to resolve these questions will require close scrutiny of conserved and convergently innervated upper

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

brainstem mechanisms as potential key components of a neural mechanism of consciousness.

ACKNOWLEDGMENTS

My gratitude goes first to all the members of the hydranencephaly internet group founded by Barb Aleman. To them and their children I owe not only this article, but a precious enrichment of my life. To Karen Krueger my thanks for permission to use photos of her daughter Heather Joy. I am grateful as well to Bernard Baars for his personal encouragement, and to him, Douglas Watt, Alan Shewmon, Jaak Panksepp, and Sunny Anand for most helpful comments on an earlier version of this manuscript. The comments and suggestions provided by five referees helped me to further improve this article. Finally, my intellectual debt to the late Eugene Sachs is gratefully acknowledged.

NOTES

1. In what follows, the term "cortex" will always be taken to mean all or part of the cerebral cortex along with its associated dorsal thalamic and claustral nuclear apparatus. The thalamic reticular nucleus, being functionally intrinsic to this thalamocortical complex is regarded as being part of it despite its embryological and phylogenetic origin in the ventral thalamus (it is directly continuous with the lateral margin of the zona incerta). Unless otherwise indicated, "subcortical" will refer to all central nervous system tissue that is not thalamocortical complex in this sense, and "brainstem" will refer to diencephalon and the rest of the entire neuraxis caudal to it.

2. To avoid possible misunderstanding of this key point, note that the analog "reality simulation" proposed here has nothing to do with a facility for simulating things such as alternate courses of action by, say, letting them unfold "in imagination," or any other version of an "inner world," "subjective thought," "fantasy," or the like. Such capacities are derivative ones, dependent upon additional neural structures whose operations presuppose those described here. The purpose of the "analog simulation" defined here is first and foremost to veridically reflect states of the world, the body, and needs at whatever level of sophistication a given species implements those realities. It is thus most directly related to the model of Philipona and colleagues (2003; 2004), as well as to the "situation room analogy" developed by Lehar (2002).

3. Note that in some of the animal and human studies cited in this passage the term "Cartesian" occurs as a misnomer for "spherical." They all refer to a system organized in terms of "azimuth" and "elevation," that is, a system of spherical coordinates.

Open Peer Commentary

The mesencephalon as a source of preattentive consciousness

DOI: 10.1017/S0140525X07000908

Francisco Aboitiz,[a] Javier López-Calderón,[a] and Vladimir López[a,b]

[a]*Centro de Investigaciones Médicas, Departamento de Psiquiatría, Escuela de Medicina, Pontificia Universidad Católica de Chile;* [b]*Department of Neurosciences, University of California San Diego, La Jolla, CA.*

faboitiz@uc.cl **http://www.neuro.cl**
javlopez@uc.cl **vlopezh@uc.cl**

Abstract: By themselves, mesencephalic subcortical mechanisms provide a preattentive kind of consciousness, related to stimulus-related, short-latency dopamine release triggered by collicular input. Elaborate forms of consciousness, containing identifiable objects (visual, auditory, tactile, or chemical), imply longer-lasting phenomena that depend on the activation of prosencephalic networks. Nevertheless, the maintenance of these higher-level networks strongly depends on long-lasting mesencephalic dopamine release.

Following and expanding on Penfield's (1952) and Thompson's (1993) ideas, Merker's provocative article proposes a central role of the upper brainstem in the mechanisms of consciousness, while the telencephalon and diencephalon serve as a medium for the increasing elaboration of conscious contents. The sensorimotor, multimodal integrative role of the brainstem is supported by large amounts of evidence, and few would argue against its key role in behavioral organization. Merker goes beyond this conception by proposing a "selection triangle," based on action selection (substantia nigra, SN), target selection (superior colliculus, SC) and motivational rating (periaqueductal gray), that controls telencephalic processing, serves to regulate behavior, and implies a conscious mode of function. In a rudimentary form, this system might be present in the earliest chordates, while the evolutionary development of the telencephalon has served to provide plasticity and to expand this system by virtue of parallel processing. An intriguing element in Merker's proposal is the role of the *zona incerta*, a GABAergic complex that is suggested to operate in competition with the SC for control of higher cortical areas.

There is no doubt that further research is necessary regarding the role of subcortical structures in conscious experience and cognitive processing in general. Cognitive neurosciences have been excessively focused on the cerebral cortex as the neural foundation of all higher psychological functions. Merker's article clearly suggests that subcortex also plays an important role deserving investigation. The compelling evidence reviewed in the target article could be not only a good inducement, but also a starting point for such research.

Our commentary is focused on the role of the midbrain superior colliculus and mesencephalic dopaminergic nuclei in orienting and goal-directed behavior (Aboitiz et al. 2006). From being originally considered to be a system that codifies reward, subsequent studies emphasized the role of the dopaminergic (DA) system in several functions like alertness, reward prediction, attention, and working memory. Behavioral and physiological approaches suggest that there are two modes of DA signaling. Tonic, longer lasting DA release may be more related to the maintenance of a goal representation in working memory, and to sustained attention during the execution of behavior (Bandyopadhyay et al. 2005; Muller et al. 1998; Rossetti & Carboni 2005; Zhang et al. 2004). On the other hand, short-latency, phasic, stimulus-related DA release (SRDR; 70–100 ms post stimulus latency, <200 ms duration) is related to unpredicted, salient stimuli and participates in updating goal representations, in attentional shifts, and in reward prediction (Montague et al. 2004; Phillips et al. 2003; Redgrave & Gurney 2006). The balance between these two systems is crucial, as failure to maintain the behavioral goal results in distractibility, and failure to update it with new sensory evidence results in perseverance (Aboitiz et al. 2006).

Several lines of evidence point to the deep layers of the superior colliculus (SC) as the main source of short-latency sensory input into the substantia nigra, be it in the context of orienting behavior toward visual stimuli (Coizet et al. 2003; Comoli et al. 2003; Dommett et al. 2005; Redgrave & Gurney 2006) or avoidance behavior in response to noxious stimuli. In the second case, aversive stimuli elicit a short-latency (<100 ms) phasic DA suppression (Ungless et al. 2004). In some contexts, SRDR works as a reward prediction device, selecting behaviors that maximize future rewards (Montague

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

et al. 2004; Schultz & Dickinson 2000; Tobler et al. 2003, Waelti et al. 2001), which is in accordance with the "action-selection" role for the SC and SN proposed by Merker.

However, in real-life conditions, the reward value of many unexpected events is unknown at the time that SRDR takes place (Redgrave & Gurney 2006). These authors consider that, perhaps more than predicting the occurrence of reward, SRDR has a role in the reselection of actions that triggered an unpredicted event. In other words, every time a salient, unexpected stimulus is produced, SRDR in the corpus striatum, amygdala, and prefrontal cortex allows an association of the sensory, motor, and contextual situations immediately previous to this event, so that the animal may develop a "causative theory" of the events that led to this unpredicted stimulus and will become able to generate them in the future (Redgrave & Gurney 2006). If this stimulus is subsequently associated with positive or negative reinforcement, the animal will know what to do in order to approach or avoid this situation, respectively.

Besides the association with contextual information, what kind of knowledge about the unpredicted stimulus itself does the animal obtain from SRDR? If the primary short-latency input to the SN is the SC, it cannot be much. Visually, mammalian collicular neurons tend to respond to spatially localized changes in luminosity that signal movement or appearance or disappearance of objects in the visual field, while being relatively insensitive to object-specific characteristics (Sparks & Jay 1986, Wurtz & Albano 1980). Furthermore, SRDR is considered to relate to pre-saccadic processing in which attention is deviated to the unattended salient event, and there is not much information about the appetitive or aversive reinforcement consequences (reviewed in Redgrave & Gurney 2006).

In agreement with Merker's proposal, conscious experience may take place in preattentive (presaccadic) stages (Koch & Tsuchiya 2007). Nevertheless, we may ask the question about what contents might this conscious function have at the collicular level. Visually, object-relevant evidence may not be fully available at this point, and it is difficult to think of a conscious process without identifiable beings or objects in it. In our view, the role of mesencephalic, subcortical mechanisms in consciousness might be better described as providing a sort of "preattentive/presaccadic conscious state," related to alertness, attentional shifts, and decision making. The participation of higher telencephalic centers is necessary to make this a sustained event into which short-term memory may participate, thus providing the essential, recursive character of higher consciousness. In this context, the longer-lasting, sustained dopamine release that supports attention and working memory may contribute to the maintenance of this kind of perception online in higher telencephalic components in order to achieve goals that are not immediately available (Aboitiz et al. 2006). In other words, Merker is quite right in assigning the mesencephalic-basal forebrain level an important role in primitive orienting and goal-directed control, which serves as a basis for a primordial, preattentive form of consciousness; but the higher telencephalic centers are necessary for the elaboration of more complex forms of behavior and recursive, object-related consciousness.

Consciousness, cortical function, and pain perception in nonverbal humans

DOI: 10.1017/S0140525X0700091X

K. J. S. Anand

Departments of Pediatrics, Anesthesiology, Neurobiology & Developmental Sciences, University of Arkansas for Medical Sciences, College of Medicine, and Pain Neurobiology Laboratory, Arkansas Children's Hospital Research Institute, Little Rock, AR 72202.

anandsunny@uams.edu

Abstract: Postulating the subcortical organization of human consciousness provides a critical link for the construal of pain in patients with impaired cortical function or cortical immaturity during early development. Practical implications of the centrencephalic proposal include the redefinition of pain, improved pain assessment in nonverbal humans, and benefits of adequate analgesia/anesthesia for these patients, which certainly justify the rigorous scientific efforts required.

A reappraisal of the mechanisms of human consciousness, differentiating it from its attributes, functions, or contents, is long overdue. Widely held concepts about the key mechanisms of consciousness, or its fullest expression via the human brain, have not been reexamined in the light of accumulating evidence since the 1970s. Merker presents the organization of a subcortical system (the centrencephalic system proposed by Penfield and Jasper in the 1950s; see, e.g., Penfield & Jasper 1954), with multiple lines of anatomical, neurophysiological, behavioral, clinical, and neuropathological evidence, and a teleological rationale – all of which support a persuasive argument for the subcortical control and temporal sequencing of behavior. Advanced neuroimaging techniques or other tools can now be applied to testable hypotheses derived from the updated centrencephalic theory, an evaluation not possible 50 years ago. One distressing impact of associating consciousness with cortical function, briefly mentioned by Merker in section 6 of the target article, pertains to the mistaken notions regarding pain perception in patient populations with impaired cortical function or cortical immaturity. Because of its clinical, ethical, and social importance, this commentary focuses on the impact of centrencephalic theory on the capacity for pain perception in subjects with impaired cortical function or cortical immaturity during early development.

Despite a higher prevalence of pain in patients with impaired cortical function (Breau et al. 2004; Ferrell et al. 1995; Parmelee 1996; Stallard et al. 2001), such patients – not unlike the children with hydranencephaly described by Merker – receive fewer analgesics as compared with matched cognitively intact patients (Bell 1997; Feldt et al. 1998; Koh et al. 2004; Malviya et al. 2001; Stallard et al. 2001). Geriatric patients with dementia also receive fewer and lower doses of opioid or nonopioid analgesics than those received by comparable, but cognitively intact elders (Bell 1997; Closs et al. 2004; Feldt et al. 1998; Forster et al. 2000; Horgas & Tsai 1998). When we consider cortical immaturity during early development, the impact of these practices appears even greater. Human neonates, preterm and full-term, were previously thought to be insensitive to pain and were routinely subjected to surgical operations without adequate anesthesia or analgesia (Anand & Aynsley-Green 1985; Anand & Carr 1989). Large numbers of newborn infants are currently exposed to painful invasive procedures without appropriate analgesia (Johnston et al. 1997; Porter & Anand 1998; Simons et al. 2003) and recent reviews have questioned the ability of premature newborns or fetuses to experience pain (Derbyshire 2006; Lee et al. 2005; Mellor et al. 2005). Clinical practices denying or discounting the pain experienced by those who have little or no self-report recapitulate the opinions of leading physicians in 19th-century America, as, for example, when "Dr. Abel Pierson, Henry J. Bigelow, and others, . . .assumed that the ability to experience pain was related to intelligence, memory, and rationality; like the lower animals, the very young lacked the mental capacity to suffer" (Pernick 1985).

The primary reasons for disregarding the experience of pain in those with limited cortical function include the current definition of pain and the exclusive association of human consciousness with cortical function.

Within the medical/scientific community, concepts of pain are based on its semantic definition rather than the actual experience it signifies. Pain is defined by Merskey and Bogduk (1994) as "an unpleasant sensory and emotional experience associated with actual or potential tissue damage, or described in terms of such damage," followed by the note that, "Pain is always subjective. Each individual learns the application of the word through

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

experiences related to injury in early life" (Merskey & Bogduk 1994). Over the years, this definition has propagated undue credibility for the verbal expression of pain, defined within the context of adult consciousness, engendering medical practices that regard verbal self-report as the "gold standard" for pain (K. D. Craig 1997; Cunningham 1998; 1999). Major flaws in this definition include its excessive reliance on verbal self-report, the criterion that some form of learning is required in order to experience pain, and its focus on use of this word rather than the experience of pain (Anand & Craig 1996; Anand et al. 1999; K. D. Craig 1997; Shapiro 1999; Wall 1997).

Confusion regarding pain perception in early life continues to hinge on various interpretations of this flawed definition (Benatar & Benatar 2001; Derbyshire 2006; Lee et al. 2005), generating a circular argument that "to experience pain, infants must first learn what is pain; to learn what pain is, they must first experience it." The experience of pain primarily informs conscious beings of bodily harm; its perception is vital to survival and cannot depend on putative memories of prior painful experiences (Anand et al. 1999; Cunningham 1999). Consistent with this rationale, even the first exposure to bodily injury demonstrates the clinical signs of pain, regardless of whether tissue damage occurs during fetal or neonatal life (Grunau & Craig 1987; Williams 2005). The experience of pain must precede any responses that ensue (verbal, behavioral, or physiological), whereas the relationships between feeling pain and reporting pain are highly context-dependent (Anand & Craig 1996; A. D. Craig 2003).

The entity of consciousness, as discussed in greater detail elsewhere (Anand et al. 1999; Benatar & Benatar 2001), is mistakenly equated with development of the human mind (Benatar & Benatar 2001; Cunningham 1998; Derbyshire 2006) and burdened with "*the expectation that living organisms must exhibit certain attributes or capabilities analogous to the adult human in order to fulfill the criteria for consciousness*" (Anand et al. 1999). Some authors argue that fetuses or neonates are not conscious, that they are complex automatons (Derbyshire & Furedi 1996; Lloyd-Thomas & Fitzgerald 1996; Zelazo 2004), simply manifesting various reflexes triggered by tissue injury, but incapable of experiencing pain because they lack consciousness or cortical maturity (Benatar & Benatar 2001; Derbyshire 2006; Lee et al. 2005; Mellor et al. 2005).

Closer examination reveals three major flaws in this scientific rationale. First, pain perception is portrayed as a 'hard-wired' system, passively transmitting pain impulses until "perception" occurs in the cortex (Derbyshire 2006; Lee et al. 2005; Mellor et al. 2005). Beginning from the Gate Control Theory of pain (Melzack & Wall 1965), accumulating evidence over the past 40 years should lead us to discard this view of pain.

Second, it assumes that fetal or neonatal pain perception must activate the same neural structures as in the adult; immaturity of these areas then supports the argument that fetuses or premature neonates cannot experience pain. However, multiple lines of evidence show that the structures used for pain processing in early development are unique and different from adults and that some of these structures/mechanisms are not maintained beyond specific developmental periods (Fitzgerald 2005; Narsinghani & Anand 2000). The immature pain system thus plays a crucial signaling role during each stage of development and therefore uses different neural elements available at specific times during development to fulfill this role (Glover & Fisk 1996).

Third, the immaturity of thalamocortical connections is proposed as an argument against fetal pain perception (Derbyshire 2006; Lee et al. 2005; Mellor et al. 2005). This reasoning, however, ignores clinical data showing that ablation or stimulation of somatosensory cortex does not alter pain perception in adults, whereas thalamic ablation or stimulation does (Brooks et al. 2005; A. D. Craig 2003; Nandi et al. 2003). The fetal thalamus develops much earlier than the cortex (Erzurumlu & Jhaveri 1990; O'Leary et al. 1992; Ulfig et al. 2000), supporting clinical observations of fetal behavior in response to tissue injury (Fisk et al. 2001; Williams 2005). Functionally specific cortical activity in response to tactile or painful stimuli in premature neonates (Bartocci et al. 2006; Slater et al. 2006) provides further evidence for the thalamocortical signaling of pain.

Functional development of the centrencephalic system very likely mediates the onset of consciousness in fetal life, defining the "being" in biological terms (Hepper & Shahidullah 1994 and Merker's target article), and enabling its responses to invasions of bodily integrity (Wall 1996, 1997).

ACKNOWLEDGMENTS

This work was supported by the National Institutes of Health (USPHS grants: U10 HD50009 and 1P20 RR018765).

Theoretical sequelae of a chronic neglect and unawareness of prefrontotectal pathways in the human brain

DOI: 10.1017/S0140525X07000921

Francisco Barceló[a] and Robert T. Knight[b]

[a]*Institut Universitari d'Investigació en Ciències de la Salut (IUNICS), Universitat de les Illes Balears, 07122 Palma de Mallorca, Spain;* [b]*Helen Wills Neuroscience Institute, University of California at Berkeley, Berkeley, CA 94720-1650.*

f.barcelo@uib.es **http://www.mcst.es/**
rtknight@berkeley.edu **http://bic.berkeley.edu/knightlab/**

Abstract: Attention research with prefrontal patients supports Merker's argument regarding the crucial role for the midbrain in higher cognition, through largely overlooked and misunderstood prefrontotectal connectivity. However, information theoretic analyses reveal that both exogenous (i.e., collicular) and endogenous (prefrontal) sources of information are responsible for large-scale context-sensitive brain dynamics, with prefrontal cortex being at the top of the hierarchy for cognitive control.

In his target article Merker reminds us of the critical role of midbrain structures for higher cognition in humans. This timely reminder should renew the interest for the study of cortical–subcortical interactions underlying human cognition. Our own research on the attentional disorders in neurological patients, although partly consistent with Merker's claims, calls for a revision of the theoretical implications of the centrencephalic hypothesis in light of the superordinate position of prefrontal cortex in the functional hierarchy of control in the human brain (Barceló & Knight 2000; in press; Barceló et al. 2000; Fuster 1997). In his otherwise very thorough review of brain anatomy and function, Merker does not consider the existence of direct prefrontotectal pathways in the human brain (Figs. 4 and 6 of the target article). In our view, this piece of anatomy carries crucial implications for computing and interpreting information processing within the central nervous system.

Direct prefrontotectal pathways have remained relatively unexplored since their discovery in primates by Goldman-Rakic and Nauta (1976). Failure to notice the relevance of prefrontotectal pathways abounds even in authoritative reviews of prefrontal anatomy (Petrides & Pandya 2002), and consequently, the putative functions of such connectivity have been overlooked or downplayed by recent models about the neural control of human cognition (Miller & Cohen 2001; Posner & Petersen 1990). This route was originally thought to aid the tracking of visual targets in spatial coordinates and was related to the cortical control of visually guided saccades and visuospatial distractibility (Gaymard et al. 2003; Pierrot-Deseilligny et al. 1991). Only recently has this route been related to the top-down control of voluntary and goal-directed behavior (Barceló & Knight 2000; in press; Friston 2005; Munoz & Everling 2004). The dorsolateral

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

prefrontal region involved, which corresponds to the middle third of the principal sulcus in the monkey, has been shown to subserve not only spatial, but also more general working memory functions closely tied in with awareness (Petrides & Pandya 2002). Hence, it seems justified to ponder the role of prefrontotectal pathways in target and action selection (sects 3.2 and 4 of the target article). In contrast to Merker's proposal of an "*anatomically subcortical but functionally supra-cortical*" system, we argue that prefrontotectal pathways evolved to allow the human prefrontal cortex to control the centrencephalic system, in line with the evolution of control architectures in the nervous system (cf. Fuster 1997).

Our argument can be substantiated by the extensive research on the neural bases of selective attention (i.e., orienting) to spatial, target, and task-set information. Most evidence for a collicular implication in target selection revolves around the selection of *the spatial location* of relatively novel, salient, or distinct perceptual objects whose abrupt onset triggers sensory and motor adjustments collectively known as an *orienting response* (Sokolov 1963). A cortical marker of the orienting response can

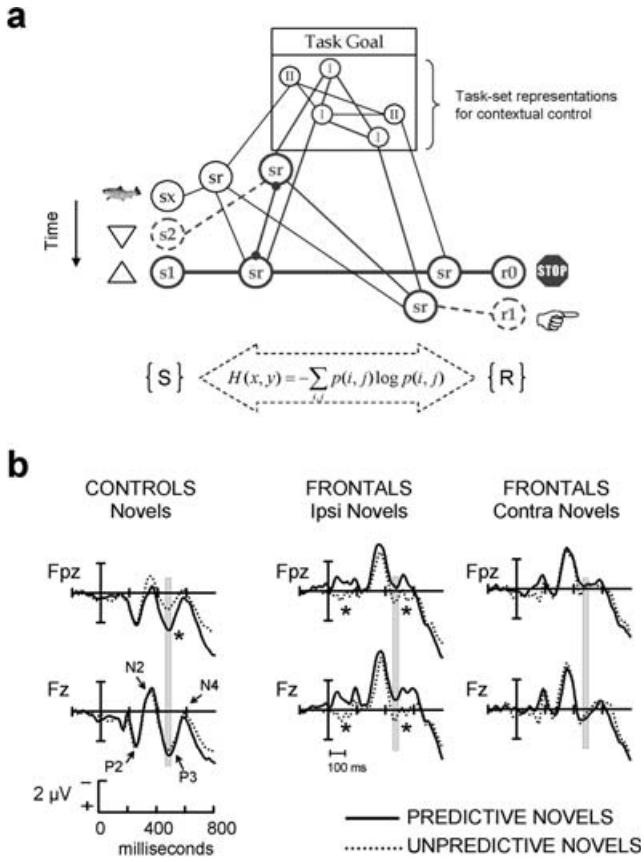


Figure 1 (Barceló & Knight). Hypothetical prefronto-tectal interactions during visual orienting to familiar and novel task-set information. (**a**) Information theoretic model of prefrontal function (adapted from Miller & Cohen, 2001). The neural representation of pools of stimulus features {S} and motor responses {R} are connected through several hierarchical levels of intervening sensorimotor processes in the central nervous system (cf. Fuster 1997). Familiar and well-rehearsed visual discriminations between upright (distracters) and upside-down (target) triangles rapidly and randomly flashed to both visual hemifields require sustained maintenance of a superordinate task-set representation (*task-set I*). This higher task-set representation holds other subordinate sensorimotor units (*sr*) in an active state at subcortical and/or posterior cortical structures, thus providing intervening pathways between perceptual and motor units. Lateral prefrontal cortex has been proposed to hold superordinate contextual representations in working memory (Miller & Cohen 2001). The onset of a familiar event triggers the updating of its corresponding sensory (*s1, s2*) and sensorimotor units (*s1-r0*, *s2-r1*) at subcortical and/or posterior cortical structures, without modifying the superordinate representation of familiar information. On the contrary, task-irrelevant unexpected novel events (*sx*) trigger an orienting response that demands updating of the active superordinate representation of task-set information (to new *task-set II*). The novel task-set II competes for attentional resources with the familiar task-set I, thus causing behavioral conflict and distractibility. When the novel event predicts the appearance of a target event in a predictable context, then a momentary conflict between two superordinate task-sets rapidly turns into anticipatory activation of the familiar task-set I, resulting in an amelioration of behavioral distractibility. (**b**) The cortical marker of the orienting response to unpredictive and predictive novel events displayed at the ipsi- and contralesion visual hemifields of patients with unilateral lesions to their dorsolateral prefrontal cortex (middle and right columns) are compared with data collapsed across both visual hemifields in controls (left column). Novel events evoked frontally distributed "novelty P3" potentials in Controls that were severely reduced in the Frontal patients regardless of the predictive value of the novel events or its visual hemifield of display. Importantly, predictive novels elicited anomalous sustained early 50–200 ms negativities over the lesioned prefrontal cortex (Ipsi Novels). The early timing of these negativities suggested conflict signals from prefrontotectal pathways that could not be dealt with because of missing superordinate task-set representations at prefrontal cortex. Grey bars indicate the time window for novelty P3 measurement. Fpz: Mid-frontopolar region; Fz: Mid-frontocentral region (for a full explanation of the task design, see Barceló & Knight 2000; Barceló et al. 2000).

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

be measured as a stereotyped scalp-recorded event-related potential, the so-called "novelty P3," which indicates that a novel event has captured attention and, at that point in time, is most likely within the focus of mind (Friedman et al. 2001). The novelty P3 potential depends on the integrity of a distributed cortical network including dorsolateral prefrontal, temporoparietal, and mesial temporal cortices (Knight & Scabini 1998). This cortical marker of the orienting response was originally described as an involuntary reaction to novel and salient stimulation reflecting modality nonspecific cortical-subcortical interactions (i.e., visual novelty P3 activations do not follow the retinotopy of the geniculostriate pathways; cf. Sokolov 1963; Friston 2005), that most likely involve faster prefrontotectal pathways (see Fig. 1b; Barceló & Knight, in press). These cortical modulations could be likened to the property of the centrencephalic system of being "symmetrically related to both cerebral hemispheres" (sect. 3.2 of the target article). New task designs and an information theoretic analytical approach have revealed more top-down cortical control in this brain's orienting response than was originally suspected (see Figs. 1a, 1b; Barceló & Knight 2000; in press; Barceló et al. 2002, 2006).

Target and action selection require integration of contextual information across the spatio-temporal dimensions of our physical world. We orient to those targets that are perceptually salient or behaviorally relevant. However, the information content of a target for perception or action depends on the learned associations between exogenous sensory signals and past short- and long-term memories and plans of action. These context-dependent associations between sets of stimuli and responses for the accomplishment of internal goals are putatively encoded at hierarchically ordered levels of representation in the nervous system (Fig. 1a). Even if the centrencephalic system has direct control over sensory (i.e., *s1*, *s2*), motor (i.e., *r0*, *r1*), and some sensorimotor (*sr*) representations needed to perform simple and familiar visuospatial discriminations, it does not seem as well equipped as prefrontal cortex for accessing the short- and long-term memories necessary for the temporal organization of human behavior (Fuster 1997). The neural decisions about whether a novel sensory signal should be selected as a target (i.e., sensorimotor pathway *s2-r1* in Fig. 1a), or inhibited as a distracter (i.e., *s1-r0* in Fig. 1a), and whether these associations are to be temporarily reversed in a different task context, demand activation of a frontoposterior cortical network for updating episodic task-set information (Barceló et al. 2002, 2006).

In a recent study (Barceló & Knight, in press), we observed that dorsolateral prefrontal cortex is necessary for establishing the contextual meaning of novel events either as irrelevant distracters in an unpredictable context (i.e., pathway *sx-r0* in Fig. 1a), or as anticipatory cues for target and action selection in a predictable context (i.e., pathway *sx-r1* in Fig. 1a; Barceló & Knight 2000; in press). Unilateral prefrontal lesions disrupted novelty P3 activity in both hemispheres regardless of the predictive value or the hemifield of novel display (Fig. 1b). Moreover, the temporal contingency between predictive novels and targets was learned *only* when novels were displayed at the ipsilesional (good) visual hemifield of patients. In this condition, predictive novels elicited anomalous sustained early 50–200 ms negativities over the lesioned cortex (Fig. 1b; Ipsi Novels). The early timing of this anomalous negativity, onsetting before visual information could reach prefrontal cortex through geniculostriate pathways, suggested incoming signals from a prefrontotectal route that could not be adequately dealt with because of missing prefrontal task-set representations. The inability to learn the novel-target contingency when predictive novels were flashed contralesionally concurs with these patients' target neglect and other superordinate deficits in cognitive control (i.e., anosognosia). From an information theoretic approach to brain function, both exogenous (i.e., collicular) and endogenous (i.e., prefrontal) sources of information are necessary to compute the informational content of sensory signals (Fig. 1a). However, the meaning of human conscious experience seems to emerge from large-scale cortical dynamics, with the prefrontal cortex acting as the chief executive in the hierarchy of cognitive control (cf. Fuster 1997).

The hypthalamo-tectoperiaqueductal system: Unconscious underpinnings of conscious behaviour

DOI: 10.1017/S0140525X07000933

Ralf-Peter Behrendt

MRC Psych, The Retreat Hospital, York, YO10 5BN, United Kingdom.
rp.behrendt@btinternet.com

Abstract: The insight that, in terms of behaviour control, the mesodiencephalic system is superordinate to the cortex should have profound implications for behavioural sciences. Nevertheless, the thalamocortical system could still be deemed an "organ of consciousness" if we came to accept that consciousness is not central to purposeful behaviour, in accordance with instinct theory. Philosophically, Merker's concepts of basic consciousness and ego-centre warrant critical discussion.

I begin with a long quote from William James' *The Principles of Psychology*, which considers the nature of self-experience in relation to action and consciousness:

> If we divide all possible physiological acts into *adjustments* and *executions*, the nuclear self would be the adjustments collectively considered; and the less intimate, more shifting self, so far as it was active, would be the executions. But both adjustments and executions would obey the reflex type … The peculiarity of the adjustments would be that they are minimal reflexes … uninteresting except through their uses in furthering or inhibiting the presence of various things and actions before consciousness … These characters would naturally keep us from introspectively paying much attention to them in detail, whilst they would at the same time make us aware of them as a coherent group of processes strongly contrasted with all other things consciousness contained – even with the other constituents of the "Self," material, social, or spiritual, as might be the case … Everything arouses them; for objects which have no other effects will for a moment contract the brow and make the glottis close … These primary reactions … are the permanent core of turnings-towards and turnings-from, of yieldings and arrests, which naturally seem central and interior in comparison with the foreign matters, apropos to which they occur, … It would not be surprising, then, if we were to feel them as the birthplace of conclusions and the starting points of acts, or if they came to appear as … the "sanctuary within the citadel" of our personal life … it would follow that all that is experienced is, strictly considered, objective; that this Objective falls asunder into two contrasted parts, one realised as "Self," the other as "not-Self;" and that over and above these parts there is nothing save the fact that they are known, the fact of the stream of thought being there as the indispensable subjective condition of their being experienced at all. (James 1890, pp. 302–304)

Merker should be applauded for emphasising the evolutionary significance of the mesodiencephalic system – comprising hypothalamus, periaqueductal gray, and superior colliculus – and pointing out that the cerebral cortex is at the service of this system. The insight that more primitive upper-brainstem-based mechanisms occupy a superordinate position in the regulation of behaviour does not mean, however, that consciousness, too, is merely elaborated by the cortex. The superior colliculus implements a form of "analog reality simulation"; however, it seems unjustified to infer that such simulation in its interaction with action representations "constitutes a conscious mode of function" formed under the influence of "feelings reflecting momentary needs" (sect. 4.2, para. 5). Reality simulation biased by motivational variables and target selection may be crucially dependent upon mesodiencephalic structures indeed, but,

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

insofar as it becomes conscious (i.e., insofar as we can speak of *feelings* and the *experience* of an external world), it may still have to involve the thalamocortical system. Consistent with psychoanalysis, behaviour is primarily instinctive, and even social behaviour remains unconscious to a large extent. Consciousness starts to play a role when behavioural impulses arising in upper brainstem systems need to be delayed and modified – with reference to past experience – to adjust to complexities and variations in the interplay between multiple and conflicting goals and unpredictable opportunities and obstacles.

If the mesodiencephalic system centred on the superior colliculus were to provide "a connective interface between the brain's basic motivational systems and the orienting machinery" (sect. 4.2, para. 7) *as well as* the connectivity needed for consciousness, how can we understand aspects or sequences of goal-directed and motivated behaviour that are unconscious? Moreover, how are we to understand forms of consciousness that are relatively uncoupled from observable behaviour and clearly unrelated to sensory information being forwarded to the colliculus (dreams and hallucinations)? Conscious experience in dreaming and wakefulness is similar phenomenologically (Behrendt 2006) and accompanied by similar patterns of thalamocortical activity (Llinas & Pare 1991; Llinas & Ribary 1993), qualifying them as fundamentally equivalent states. In dreams and hallucinations, thalamic relay cells are less responsive to sensory stimulation while brainstem-based arousal mechanisms continue to activate thalamocortical circuits (Behrendt 2003). Here, conscious experience is uncoupled from sensory input representing the external world, and it seems unlikely that changes in thalamocortical activity elaborating the content of conscious experience in these states are paralleled by *corresponding* activity changes in the superior colliculus, in contrast to Merker's testable prediction, although the inferior colliculus was active during auditory hallucinations (Shergill et al. 2000).

Merker's hypothesis crucially depends on the notion that consciousness is "the 'medium' of any and all possible experience" (sect. 1, para. 3), and therefore that consciousness can be separated from the content of experience – that there can be consciousness without content. Indeed, he treats consciousness as a "functional utility" that is "independent of the level of sophistication at which the contents it integrates are defined" (sect. 1, para. 6); and it is only from this position that we can interpret Penfield and Jasper's (1954) findings as suggesting that "hemispherectomy does not deprive a patient of consciousness, but rather of certain forms of information, discriminative capacities, or abilities, but not of consciousness itself" (sect. 2, para. 3). This position may also misguide us to look for a "way in which this medium might be implemented neurally" (sect. 1, para. 4); and when pinning primary consciousness to "quite specific neural arrangements" one comes to the rather paradoxical conclusion that anencephalic children who "show responsiveness to their surroundings in the form of emotional or orienting reactions to environmental events" (sect. 5, para. 6) – such as sounds and "salient visual stimuli" – are conscious, whereas purposefully reacting invertebrates, such as the medusa, which lack such "specific structural arrangements" (sect. 1, para. 4) are not.

What is more problematic is that by *reducing* consciousness to "the kind of responsiveness to their surroundings that qualifies as conscious by the criteria of ordinary neurological examination" (sect. 5, para. 4), Merker ignores the subjective nature of conscious experience (Searle 1992, 1997). Signs of pleasure or excitement exhibited by anencephalic children are not necessarily indicative of conscious experience and can only impress the reductionist as "a weighty piece of evidence regarding their conscious status" (sect. 5, para. 7). They may be regarded more parsimoniously as automatic "molar" behaviour patterns represented in mesodiencephalic structures and activated by suitable stimuli. The fact that some patients with damage to the striate cortex can recognise or discriminate visual stimuli presented in their blind visual field in the absence of awareness (blindsight) (Weiskrantz 1996) illustrates that "environmental sensory information is related to bodily action (such as orienting)" (sect. 5, para. 10) *not* necessarily through the medium of a "primary consciousness." Decorticate animals orient to their surroundings and display molar behavioural reactions, suggesting indeed that these behaviours are dependent on structures in the mesodiencephalic region, but they too may do so without conscious awareness. Cortical blindness following destruction of posterior cortical visual areas can be restored by inactivation of the contralateral superior colliculus (Sprague effect); however, the restoration in the formally blind field is "limited essentially to the ability to orient to and approach the location of moving visual stimuli" (sect. 3.1, para. 1), so that we cannot be confident that the orienting behaviour now under control of the ipsilateral superior colliculus is conscious, that is, that we are dealing with a "partial restoration of vision" (sect. 3.1, para. 2) in the sense of a conscious function.

Merker appreciates that "what we confront in sensory consciousness is indeed a simulated (synthetic) world and body" (sect. 4.3, para. 5), concurring with philosophical idealism (Behrendt 2006). Problematic, however, is the notion of "egocenter" (sect. 4.3), which "we ourselves occupy when we are conscious" (sect. 4.3, para. 2) and which is thought to be located at the "origin of the coordinate system of the simulation space" (sect. 4.3, para. 2). Passivity phenomena in schizophrenia suggest that there is *no* "irreducible asymmetry . . . between perceiving subject and apprehended objects" (sect. 4.3, para. 2). More likely, basic sensorimotor self experience is a *derivative* of instinct-driven conscious behaviour: Tension reduction during approach to a desired goal – the yielding to an urge or impulse, often after overcoming conflicting drives – which accompanies all consciously guided behaviour and thinking, introduces an asymmetry between self and non-self into the unitary realm of subjective conscious experience (Behrendt 2004; 2005), which according to philosophical phenomenology and idealism is all that is available to us (see the quotation from James [1890] at the beginning). We are, in other words, not "central residents of that simulation" and as such "subject to ever shifting moods, feelings, urges, emotions, and impulses" (sect. 4.3, para. 6), but we ourselves are the product of these urges, emotions, and impulses (Behrendt 2004; 2005). The postulation of "an inherently 'perspectival,' viewpoint-based, relation to the contents of sensory consciousness" (sect. 4.3, para. 2) is unnecessary and *does not* accord with what Schopenhauer (1819/1958) meant when he stated that the subject as the *bearer of the world* is in itself unknowable – that the knowing and representing subject (the material underpinnings of the realm of conscious experience) cannot be found in the world that is experienced (Behrendt 2006).

Subcortical consciousness: Implications for fetal anesthesia and analgesia

DOI: 10.1017/S0140525X07000945

Roland R. Brusseau[a] and George A. Mashour[b]

[a]*Department of Anesthesia, Perioperative and Pain Medicine, Children's Hospital, Harvard Medical School, Boston, MA 02115;* [b]*Division of Neurosurgical Anesthesia, Department of Anesthesiology, University of Michigan Medical School, Ann Arbor, MI 48109.*

roland.brusseau@childrens.harvard.edu

gmashour@med.umich.edu

Abstract: In this commentary we discuss the possibility of subcortical consciousness and its implications for fetal anesthesia and analgesia. We review the neural development of structural and functional elements that may participate in conscious representation, with a particular focus on the experience of pain.

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Is a cortex required for consciousness? If we adopt the view of Hameroff (2006) that consciousness in its most basic form may be considered "minimal awareness" without a requirement for memory, cognition, or organizational sophistication, then Merker makes a compelling argument that subcortical structures are both necessary and sufficient. In this context Merker discusses the ethical administration of anesthesia and analgesia to children with hydranencephaly, as well as neonates. In an era in which prenatal interventions are increasingly common, such ethical questions now apply to the developing fetus. If a fully mature cortex is not required for consciousness, at what point in development can the fetus potentially feel pain? Within Merker's paradigm, the possibility of fetal pain depends on the development of the structural and functional apparatus for subcortical processing. If we consider "pain" to be the coordinated, subjective experience of nociception, then "pain" may serve as a functional surrogate for consciousness. Analysis of the development of pain pathways may inform our understanding of the structural and temporal development of consciousness itself.

The first essential requirement for nociception and pain is the presence of sensory receptors, which develop first in the perioral area at around 7 weeks gestation. From 11 weeks, they develop in the rest of the face and in the palmar surfaces of the hands and soles of the feet. By 20 weeks, they are present throughout all of the skin and mucosal surfaces (Smith 1996). The nociceptive apparatus is initially involved in local reflex movements at the spinal cord level without supra-spinal integration. As these reflex responses become more complex, they subsequently involve the brainstem, through which other responses, such as increases in heart rate and blood pressure, are mediated. Such reflex responses to noxious stimuli have not been shown to involve the cortex and, thus, traditionally have not been thought to be available to conscious perception (Myers & Bulich 2005). Merker's article brings this into question.

Penfield and Jasper (1954), however, suggest that cortical structures are at least in some way required. The subcortical system – including the basal ganglia, medial thalamus, ventrolateral thalamus, substantia nigra, ventral tegmental area, superior colliculus, median raphe, and the midbrain and pontine reticular formation – does not function "by itself alone, independent of the cortex," but "by means of employment of various cortical areas" (Penfield & Jasper 1954, pp. 473–74; see target article, sect. 2, para. 7). Therefore, if integrative thalamic function is necessary for nociceptive perception (i.e., "pain") or any other higher-order sensory perception, it cannot be until the thalamocortical connections are formed and functional. The thalamus is first identified in a primitive form at day 22 or 23 postconception. Its connections grow out in phases, initially only as far as the intermediate zone of the cerebral wall, collecting below the cortical plate. The neurons then advance further into the cerebral hemispheres, eventually becoming localized into their specific functional fields. The final thalamocortical connections are thought to be in place by around 26 weeks, although estimates differ (Royal College of Obstetricians and Gynecologists 1997). In fact, there are thought to be transient cholinergic neurons with functioning synapses connecting the thalamus and cortical plate from approximately 20 weeks (Kostovic & Rakic 1990). This point could be considered the absolute earliest time in gestation when a fetus could be aware of nociceptive stimuli.

The presence of electroencephalographic (EEG) activity would suggest a degree of *functional* maturity, in addition to *structural* maturity, of neural systems mediating consciousness. While sporadic electrical activity has been detected in the fetal brain as early as 43 days gestation (Holzman & Hickey 2001), more coordinated electrical activity (in the form of intermittent bursts) has been shown to be present in the brainstem from 12 weeks, and the cerebral hemispheres at 20 weeks (Myers & Bulich 2005). Before 25 weeks, the electrical activity on EEG recordings is discontinuous, with periods of inactivity lasting up to 8 minutes and bursts of activity of only 20 seconds (accounting for only 2% of the total time). From 25 to 29 weeks, the periods of activity increase, such that by 30 weeks, although EEG activity is still not continuous, distinct patterns of wakefulness and sleep can be recognized as the precursors of adult patterns. These are not initially concordant with behavioral state; over the next few weeks, however, the degree of concordance improves (Clancy 1998). By 34 weeks, electrical activity is seen 80% of the time; from 34 to 37 weeks, sleep/wake cycles become more defined (Myers & Bulich 2005).

Although current studies cannot provide direct evidence of fetal consciousness, they do suggest that the required neural processing architecture may be in place and functional. If we are to accept that by approximately 20 weeks the requisite neural substrate of consciousness (e.g., the thalamus and associated subcortical structures) and its proper connections are in place and accompanied by a coordinating EEG rhythm (even if only intermittently), what can we say about the beginning moments of fetal consciousness? Again, it would seem that we can conclude that consciousness is at least *possible* from this point forward in fetal development. If a more stringent threshold for continuous EEG activity is required, then it would appear that by 30 weeks gestation, when patterns consistent with wakefulness and sleep may be discriminated, consciousness is at least *possible*.

If we accept that a subcortical consciousness is possible by 20 weeks (or, more conservatively, 30 weeks), then it also would appear possible that fetuses could experience something approximating "pain." Surely, the complex behavioral responses seen in ventilated neonates have the external appearance of pain, but because we currently have no metric with which to make such a determination, we cannot know this with any certainty. The mere *possibility* of consciousness and an experience of pain – however rudimentary – would mandate a provision of appropriate anesthesia and analgesia. Merker would appear to agree, as the evidence surveyed in his article gives no support for consciousness as an exclusively cortical function. Rather, he implies that subcortical structures may be necessary and sufficient to generate consciousness and, therefore, a rudimentary experience of pain. As such, his challenge to the medical community has significant ramifications for medical ethics, as well as the provision of fetal anesthesia and analgesia.

Consciousness without a cortex, but what kind of consciousness is this?

DOI: 10.1017/S0140525X07000957

Anton M. L. Coenen

NICI, Department of Biological Psychology, Radboud University Nijmegen, 6500 HE Nijmegen, The Netherlands.

a.coenen@nici.ru.nl

Abstract: Merker suggests that the thalamocortical system is not an essential system for consciousness, but, instead, that the midbrain reticular system is responsible for consciousness. Indeed, the latter is a crucial system for consciousness, when consciousness is regarded as the waking state. However, when consciousness is regarded as phenomenal consciousness, for which experience and perception are essential elements, the thalamocortical system seems to be indispensable.

Structures in the upper brainstem mediate consciousness by activation and arousal of the entire thalamocortical system, thus producing the waking state. When the mesencephalic reticular formation becomes active, the activity in the thalamocortical loops rise, together with an opening of the sensory channels. A stream of information from the outside world flows to the higher brain centers and is perceived. Numerous neuronal systems start to process and integrate this information and the

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

activity of myriads of neurons firing in the tonic mode is expressed in consciousness, a sort of neural orchestra. It is a common assumption that the neuronal basis of consciousness results from the interactive processes between the brain stem reticular formation and the thalamocortical system (Coenen 1998).

When the activity of the mesencephalic reticular formation drops under a critical level, an inhibitory system becomes active and starts to inhibit the thalamocortical neurons. Then, these neurons are tied together by the inhibitory interneurons and discharge irregularly in a burst-pause mode. Slow wave sleep is the result. Because of "thalamic gating," sensory information is largely blocked during sleep and information processing is at a low level. Perceptive processes are minimal and consciousness is also at a low level (Coenen 1998). The interaction between the midbrain reticular formation, the nonspecific diencephalic nuclei and the thalamocortical system seems to control the high consciousness during sleep and the low consciousness during slow-wave sleep.

Absence epilepsy is a form of non-convulsive epilepsy, occurring in children as well as in animals. The basic characteristic of this type of epilepsy is the reduction in responsiveness and consciousness, associated with spike-wave discharges in the electroencephalogram. The "centrencephalic" theory suggests that these aberrant brain discharges originate from a deep-seated intrathalamic pacemaker extending to the midbrain reticular formation (Penfield & Jasper 1954), whereas recent research points towards a prominent role for the cortex in this process (Meeren et al. 2005). Absence seizures are characterized by lapses in consciousness and a lack of response towards external stimuli. Absence seizures share many similarities with slow-wave sleep (Coenen 1999). Already mentioned is the reduction in consciousness and the unresponsiveness to sensory stimulation. Despite the reduction in responsiveness, both states can be terminated by strong stimuli. Another correspondence is that unconscious stimulus evaluation still seems possible. Relevant stimuli can terminate both slow-wave sleep and absence attacks more easily than neutral stimuli. This also shows that some consciousness is still present during both states. Presumably, all phenomena can be related to the underlying neuronal mechanisms. In both the sleep state and the absence state, neurons are firing in the "burst firing" mode. A difference is the regular and spiky character of the spike-wave discharges, which could be a result of the even stronger burst firing mode during absences (Coenen 1995). The midbrain reticular formation is inhibited in both states, which implies a reduction in consciousness. A firm conclusion is inevitable: an active midbrain reticular system is a necessary condition for consciousness. This agrees well with the conclusion of Merker.

But what is the role of the thalamocortical system in consciousness and can consciousness exist without the thalamocortical system? These are the intriguing questions faced by Merker. He concludes that the thalamocortical system cannot alone be regarded as "the organ of consciousness"; instead, it is the "centrencephalic system" or midbrain reticular system that seems to play main fiddle in consciousness. Or in Merker's own words "brainstem mechanisms are integral to the constitution of the conscious state" and "neural mechanisms of conscious function cannot be confined to the thalamocortical complex alone" (target article, Abstract). One of the central questions, however, is what Merker means by consciousness. Despite several explanations, the meaning of this hard to define and difficult concept is not clear to all. Zeman (2001), in his extensive review, distinguishes from among the eight meanings of consciousness, two principal meanings. The first is, "consciousness as the waking state" and the second is, "consciousness as experience." Consciousness in the first sense is the behavioral expression of the waking state. Being conscious in that sense is synonymous to being alert and awake. The second sense of consciousness, however, refers to becoming aware of something and to experience something, which is often called "phenomenal consciousness" (Block 1995). The essence of phenomenal consciousness is inextricably bound up with experience and perception, for which the thalamocortical system is mainly responsible. Philosophers often use the term "qualia" to highlight the subjective dimensions of experience and perception. Consciousness in the first meaning (consciousness as the waking state), is in this view a necessary condition for consciousness in the second sense (consciousness as experience or phenomenal consciousness).

Going back to the meanings of consciousness in the interaction of the midbrain reticular and thalamocortical systems, the following picture emerges. The midbrain reticular system takes care of wakefulness and arousal, it brings the thalamocortical system into a state conducive for experience and perception, leading to the processing and integration of information, and thus to consciousness in the second sense. The midbrain reticular system acts as the medium for phenomenal consciousness. It forms the engine of the car, while the vehicle itself (the thalamocortical system) is necessary for driving the car. Hence, I agree with Merker's view that consciousness can exist without a cortex, and at the same time I disagree with Merker's view that consciousness can exist without a cortex. It depends on the type of consciousness. Waking consciousness is possible with the midbrain reticular system alone, but phenomenal consciousness is not possible without the thalamocortical system. Two intact systems are necessary for consciousness: the midbrain system for waking and vigilance (the engine), and the thalamocortical system for perception and experience (the vehicle). That children without a cortex may experience some phenomenal consciousness, might be explained by the fact that parts of the extensive thalamocortical system are still functional.

Do multiple cortical–subcortical interactions support different aspects of consciousness?

DOI: 10.1017/S0140525X07000969

Daniel Collerton[a] and Elaine Perry[b]
[a]*Northumberland, Tyne, and Wear NHS Trust, Bensham Hospital, Gateshead NE8 4YL, United Kingdom;* [b]*Wolfson Research Centre, Institute for Ageing and Health, Newcastle General Hospital, Newcastle-upon-Tyne NE4 6BE, United Kingdom.*
daniel.collerton@ghnt.nhs.uk **e.k.perry@ncl.ac.uk**

Abstract: Merker's core idea, that the experience of being conscious reflects the interactions of actions, targets, and motivations in the upper brainstem, with cortex providing the content of the conscious experience, merits serious consideration. However, we have two areas of concern: first, that his definition of consciousness is so broad that it is difficult to find any organisms with a brain that could be non-conscious; second, that the focus on one cortical–subcortical system neglects other systems (e.g., basal forebrain and brainstem cholinergic systems and their cortical and thalamic target areas) which may be of at least equal significance.

Bjorn Merker has to be admired for entering the debate on the question of the location of consciousness with the bold assertion that the cortex is not essential. His core proposal, that the experience of being conscious reflects the interactions of systems supporting actions, targets, and motivations in the upper brainstem, with cortex providing the content of the conscious experience, is novel. It seems highly likely that upper brainstem systems projecting to the superior colliculus are important components of integrative networks that support consciousness in mammals. However, we argue that they are neither quite so critical nor as unique as he suggests.

One area of concern is that Merker's use of the term "consciousness" is too broad to allow a clear focus on specific brain areas. The definition of consciousness as being a "state or activity

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

that is characterized by sensation, emotion, volition, or thought" (sect. 1) could include, in its most basic sensation form, receiving, processing, and responding to any environmental signal or information. Such a definition is applicable not only to mammals, but also to most animals with a cerebrum, no matter how different from humans (Edelman et al. 2005). Innumerable nonliving mechanisms might also fit the bill.

Such a very broad use of the term "consciousness" both undermines Merker's use of mammalian evolutionary homologies to support his localisation in the brainstem and weakens the importance of his evidence from children born without a cortex. We entirely agree on the need to see each child's individual capabilities and not draw conclusions from diagnostic labels. However, his scientific case would be strengthened if he could show that there was no relationship between variations in consciousness and residual amounts of cortex. The more restricted use of the term "consciousness" that he later seems to favour, involving subjective awareness (more analogous to self awareness in Morin's 2006 taxonomy), may localise to a smaller range of neurobiological structures.

Merker uses evidence of consciousness in the absence of cortex in rats and children to argue that brainstem structures are of primary importance to the conscious experience. However, this data is also consistent with consciousness being the product of a resilient distributed neural network (or network of networks). Arguing against a single consciousness system, damage in restricted brain areas – for example, from strokes (Goldstein & Simel 2005), provided arousal is not grossly impaired – rarely abolishes consciousness entirely, though it may well limit the areas to which it can be applied. Thus, unilateral spatial neglect (sect. 3.1) suggests that consciousness can be fractionated, at least in space, and perhaps in modality.

In order for upper brainstem systems to be especially relevant within these networks, Merker would have to show that lesions within the superior colliculus, for example, have profound effects on consciousness. However, collicular lesions generally impair orienting rather than consciousness (sect. 4.5, see also Burnett et al. 2004), and the gross disturbances in consciousness common after brainstem strokes are due to the disruption of the ascending cholinergic and other projections, which we discuss further on.

The neuropathology of diseases that disturb consciousness can provide important insights. Parkinson's disease (PD) with its relatively specific nigral dopaminergic loss, which leads to gross basal ganglia dysfunction, can test the role of the basal ganglia input to the superior colliculus within his model. Pathology in this system does lead to eye-blink abnormalities (Basso et al. 1996) and, consistent with Merker's hypothesis, visual hallucinations (a disorder of the content of consciousness), and disturbed dream content and behaviour occur in PD, as well (Olson et al. 2000; Onofrj et al. 2006). (We consider that dreaming is a normal state of altered consciousness). However, such disorders of consciousness are even more closely associated with the related disorder, Dementia with Lewy Bodies (DLB; Boeve et al. 2004; Collerton et al. 2005). Additionally, the fluctuating basal ganglia function in PD leads primarily to fluctuating motor symptoms (Denny & Behari 1999); not to the fluctuations in consciousness that are seen in DLB (Bradshaw et al. 2004; Walker et al. 2000). Pathology in DLB extends far beyond Merker's brainstem system, and includes clinically relevant disturbances in cholinergic systems (Fujishiro et al. 2006; Lippa et al. 1999; Perry et al. 1993; Tirabosci et al. 2002; Ziabreva et al. 2006), which may also be important in conscious experience.

The basal forebrain cholinergic system, with its multiple projections to GABA and glutamate neuronal networks in the cortex and thalamic regions, and its role in both tonic and phasic activation via specific nicotinic and muscarinic receptor subtypes is, in conjunction with cholinergic projections from the brainstem to key areas such as thalamus and substantia nigra, a candidate integrative mechanism underpinning the emergence of consciousness from unconscious mental activity (Perry et al. 1999).

Dreaming and anaesthesia also support a central role for the interaction of cholinergic projections and cortical target areas in modulating conscious awareness. Between sleep (non-REM and REM) and waking, alterations in basal forebrain cholinergic activity correlate with concomitant changes in consciousness, to a greater extent than in monoaminergic and other systems (Perry & Piggott 2000). Among drug-induced changes in consciousness, mechanisms of general anaesthetic-induced disruption of the effective connectivity and integrative processes required for consciousness is considered likely to provide insights into neural correlates of consciousness (Mashour 2006). It is well established that neuronal nicotinic acetylcholine receptors are particularly sensitive to inhalational anaesthetics (Rada et al. 2003). For example, isoflurane, sevoflurane, and halothane potently block the $\alpha 4\beta 2$ nicotinic subtype (Yamashita et al. 2005). Alterations in the same nicotinic receptor subtype in temporal cortex and thalamus are related to disturbances in consciousness in DLB (Ballard et al. 2002; Ray et al. 2004; Pimlott et al. 2006).

We have argued that brainstem and basal forebrain cholinergic projections to the ventral visual stream, lateral frontal cortex, and connecting structures (Collerton et al. 2005, Fig. 7) form a distributed system for conscious visual processing (Collerton et al. 2005, Fig. 3). Dysfunctional conscious awareness – visual hallucinations – can result from subcortical cholinergic dysfunction incorrectly modulating the balance between top-down and bottom-up processing within the cortex. The disturbance, in this case, therefore lies within a cortical–subcortical system distinct from that described by Merker.

Consistent with a cholinergic component of consciousness and the suggestion that Merker's system is one among many supporting consciousness, not only the superior colliculus but other key "hub"/central station areas in the brain that collect a multiplicity of afferents from and distribute efferents to essential areas such as brainstem, thalamus, or cortex (e.g., interpeduncular nucleus, many thalamic nuclei, in particular the lateral geniculate, the substantia nigra pars compacta, and the septum, subiculum, and parahippocampal gyrus) are relatively very high in nicotinic receptors; especially $\alpha 4\beta 2$ (Han et al. 2003; Perry & Kellar 1995; Perry et al. 1993; 1995; Spurden et al. 1997) which facilitates GABA inhibition (Endo et al. 2005).

We therefore conclude that Merker has not quite made his case that the cortex is inessential in conscious experience, but that he has very helpfully provided a new focus on the need to incorporate subcortical mechanisms as well.

Pain, cortex, and consciousness

DOI: 10.1017/S0140525X07000970

Marshall Devor

Department of Cell and Animal Biology, Institute of Life Sciences and Center for Research on Pain, Hebrew University of Jerusalem, Jerusalem, 91904, Israel.
marshlu@vms.huji.ac.il

Abstract: Painful stimuli evoke functional activations in the cortex, but electrical stimulation of these areas does not evoke pain sensation, nor does widespread epileptic discharge. Likewise, cortical lesions do not eliminate pain sensation. Although the cortex may contribute to pain modulation, the planning of escape responses, and learning, the network activity that constitutes the actual experience of pain probably occurs subcortically.

Pain is a sensory and emotional quality experienced by a conscious brain. There has never been much doubt that the pathways leading to pain perception, like all other conscious

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

experience, end in the cerebral cortex. However, closer consideration of this dogma raises some perplexing questions.

Microelectrode recordings in animals, and noninvasive functional imaging in humans, show excitations in many brain areas following pain-provoking stimulation of the skin and internal organs (Peyron et al. 2000). These include structures long known as key parts of the somatosensory system, such as the thalamic nuclei VPL-VPM and S1 and S2 cortex, as well as areas not classically thought of as somatosensory processors, such as the cerebellar cortex and the corpus striatum. Curiously, the most robust and reliable cortical activations occur not in S1 and S2 but in limbic cortical areas, including the anterior cingulate cortex (ACC) and the posterior insular cortex. Noxious stimulation of different organs – skin versus viscera, for example – reveal different if overlapping patterns of cortical activation, appropriate to the different "feels" evoked. Moreover, these cortical activations, particularly in ACC, track reported pain unpleasantness and not the intensity of the applied stimulus when the two are dissociated by manipulations such as placebo and hypnotic suggestion (Rainville et al. 1997; Strigo et al. 2003).

All of these observations are as expected of a cortical pain analyzer. However, other observations are not as expected. The most important is that direct electrical stimulation of the cortical convexity, including areas activated by painful stimuli, almost never evokes a report of pain in awake patients (Libet 1973; Penfield & Rasmussen 1955). Likewise, for transcranial magnetic stimulation (TMS). This contrasts with stimulation of cortical areas associated with vision, hearing, smell, and (non-painful) touch, which readily arouses the corresponding percepts. It may be argued that the structures relevant for pain sensation are buried in the mid-sagittal (ACC) or Sylvian sulci (insula) and are hard to access by surface stimulation. A related explanation is that unlike the other senses, multiple cortical areas must be activated simultaneously to evoke a sensation of pain. However, in epileptic seizures cortical discharge is frequently widespread and includes, indeed often favors, these buried limbic cortices. Nonetheless, it is very rare for epilepsy to include auras that are painful (Nair et al. 2001). A recent report of pain evoked in a small number of epileptic patients by depth electrodes on the insular cortex is a potential exception (Mazzola et al. 2006). However, it has been shown that direct stimulation of the meninges and blood vessels that overly the insular cortex evokes pain sensation (Pereira et al. 2005). These structures have rich nociceptive innervation from the trigeminal ganglion. Thus, the claim that pain is evoked by insular stimulation using depth electrodes may be confounded by inadvertent simultaneous stimulation of local non-neural tissues. That is, the reports of pain on insular stimulation may not actually be due to activation of the insular cortex. Note that in contrast to the cortex, pain is readily evoked by focal (microelectrode) stimulation in certain areas of the thalamus and brainstem (Dostrovsky 2000).

Another retort sometimes given in response to the question of why cortical stimulation is so rarely painful is that pain is complex and is multiply represented in the cerebral hemispheres. As a consequence, unlike vision, hearing, smell, and touch, to evoke pain by cortical stimulation would require precisely patterned stimulation, simultaneously, at many locations. This condition is neither met by Penfield-type stimulation experiments, nor is it found in natural seizures. However, if evoking a pain percept requires such precise, complex, and necessarily fragile patterning of activity, then disruption of the pain network at any of numerous loci ought to eliminate the ability of natural stimuli to evoke pain sensation. In fact, focal lesions in cortical areas active during pain, and even massive cortical lesions, do not produce analgesia. On the contrary, cortical strokes are often followed by chronic neuropathic post-stroke pain (Boivie et al. 1989). Lesions in cortical areas thought to subserve vision, hearing, smell, and touch do not behave in this way. Patients with large lesions in the primary visual cortex, for example, are perceptually blind, although they may have some residual visually guided function. Why, then, do large lesions in the somatosensory areas of the cortex, or any cortical region for that matter, not render people "blind" to noxious stimuli, that is, make them pain-free?

These observations demand that one at least consider the possibility that the neural computations that generate pain experience play out subcortically rather than in the cerebral cortex. Certainly, focal electrical stimulation at many subcortical sites, from the spinal cord to the thalamus, is able to provoke pain sensation. Patients with lesions in the right parietal cortex sometimes show sensory neglect, denying that a body part (arm, leg) belongs to them. However, noxious stimulation of the denied limb evokes normal wincing, autonomic responses, and withdrawal. Pain is experienced and acknowledged, but is missing a location in the body schema. Finally, people with massive cortical lesions that qualify them for the diagnosis "persistent vegetative state," anencephalic children, and decorticated animals, all show organized, adaptive "nocifensive" behavior in response to noxious stimuli. True, such behavior, in itself, does not prove that the noxious stimulus has been experienced as pain by a conscious brain. It only proves that the noxious stimulus has been registered and basic adaptive motor sequences have been generated in response. Nonetheless, in light of the possibility that pain perception does not require cortical function, a decision to end the life of a vegetative patient ought to be carried out painlessly using a fast-acting agent, rather than by withholding life support and condemning the patient to a month or more of starvation.

Corticothalamic necessity, qualia, and consciousness

DOI: 10.1017/S0140525X07000982

Sam M. Doesburg and Lawrence M. Ward

Department of Psychology, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada.

sam@psych.ubc.ca **http://www.psych.ubc.ca/~lward/**
lward@psych.ubc.ca **http://www.psych.ubc.ca/~lward/**

Abstract: The centrencephalic theory of consciousness cannot yet account for some evidence from both brain damaged and normally functioning humans that strongly implicates thalamocortical activity as essential for consciousness. Moreover, the behavioral indexes used by Merker to implicate consciousness need more development, as, besides being somewhat vague, they lead to some apparent contradictions in the attribution of consciousness.

Merker has done an excellent job of bringing the centrencephalic proposal of Penfield and Jasper up to date. We wish to sharpen the contrast between Merker's updated proposal and the proposal that the thalamocortical system, instead, constitutes the fundamental neural substrate of consciousness. The possibilities regarding the respective roles of the mesodiencephalic system described by Merker and thalamocortical system are three: either one, or the other, or both are necessary and sufficient for the existence of the conscious state. In this commentary we adumbrate evidence that the thalamocortical system is necessary, if not sufficient, for conscious awareness as experienced by humans. These data are difficult to account for in the mesodiencephalic proposal, as are, in turn, some data discussed by Merker for the thalamocortical proposal. An unsatisfying but reasonable conclusion is that both systems play crucial roles in the generation of the conscious state.

Merker argues for the existence of consciousness in humans without a cerebral cortex, at least partly, on the basis of the behavior of hydranencephalic children who "are not only awake and often alert, but show responsiveness to their surroundings in the form of emotional or orienting reactions to environmental

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

events [. . .], . . . express pleasure by smiling and laughter, and aversion by 'fussing,' . . . and show preferences for certain situations and stimuli over others" (target article, sect. 5, para. 6). Earlier, the cubomedusa is given as an example of a species that cannot possess consciousness because of its simplistic, non-cephalized, nervous system architecture. Cubomedusa, like other even simpler organisms such as *C. elegans* (e.g., Rankin 2002), should display responsiveness to external stimuli, approach and aversion, and conditioned preferences for certain stimuli and situations (although many of these experiments appear not to have been done for cubomedusa). It *does* display coordinated mating and hunting behavior as well as avoidance of particular obstacles (e.g., Coates 2003). If the cubomedusa can display such behaviors without consciousness, then so, perhaps, can hydranencephalic humans.

Conversely, it has been proposed that the nerve ring that connects ganglia near the eyes and swimming effectors in the cubomedusa serves to integrate visual information for action in the most effective way for a radially symmetric organism (Coates 2003). If behaviors such as those listed earlier indicate the capacity for conscious experience, and given its nerve ring mechanism to provide neural integration, it seems possible that even the cubomedusa experiences its visual environment in a crude and primitive way. Thus, cephalization might not be necessary for conscious experience.

Neither of these conclusions is particularly palatable, although each is reasonable and potentially correct. The difficulty in finding useful behavioral indicators underscores the importance of centering our inquest into the neural correlates of consciousness where we can be most certain about whether consciousness is present, namely, in neurologically normal adult humans or in human subjects in which brain damage has resulted in a reportable loss of consciousness. Disorders of awareness reveal some inconsistencies with the mesodiencephalic theory of consciousness that need to be accounted for. Consider, for example, cortical blindness, or "blindsight," which is a loss of visual awareness induced by damage to the striate cortex. Residual *nonconscious* visual functions in blindsight have been attributed to the superior colliculus and its inputs to the cortex (Leh et al. 2006). Hence, in otherwise normally conscious humans, it seems that the visual and other information that is integrated in the superior colliculus *is not* consciously available. The Sprague effect does not resolve this issue, because what is recovered are subcortically mediated orienting responses similar to those demonstrated in blindsight. Thus, blindsight and similar pathologies (e.g., cortical deafness) constitute evidence for an apparent reliance of conscious experience on processing in the corticothalamic system.

A central tenet of the midbrain theory of consciousness is that, within the midbrain, a "winner take all" system exists, thereby accounting for the dynamic and integrated/unified stream of consciousness, furnished with the most salient perceptual and motor information. One problem with this idea is that the neural representations in the midbrain network do not possess the detail characteristic of human experience. Clear examples can be taken from the qualia of vision. Only in the cortex do representations possess sufficient definition in terms of form, motion, color, and spatial resolution to account for human qualia. Indeed, the complexity and integration inherent to processing in the thalamocortical system has been proposed to be essential for consciousness (Tononi 2004; Tononi & Edelman 1998). Descending afferents to the superior colliculus result in representations in which sufficient information reduction has occurred to make them inconsistent with the fine grain of our experience. Although midbrain systems could be sufficient for a crude and primitive form of consciousness, it is unclear how this system could account for the everyday consciousness of adult humans. Does the corticothalamic system "take over" as the seat of consciousness in normal adults? Does the seat of consciousness now extend to a larger section of the brain? Are the various representation levels overlaid upon one another, and only the most detailed level experienced, as proposed by Brown (1988)? Here the Sprague effect in relation to blindsight should be reconsidered, as what is *not* recovered are functions requiring the more detailed representations characteristic of our qualia, such as pattern recognition (Loop & Sherman 1977).

Moreover, as much cortical activity is not experienced, there also must be a "winner take all" network in the cortex. Transient large-scale networks of synchronous neuronal oscillations, proposed as being a mechanism that underlies feature binding in sensory awareness (Engel & Singer 2001), could also operate to select a subset of cortical activity for integration into a conscious representation (Varela et al. 2001). Such a network could be responsible for excluding V1 activity, for example, from direct experience (e.g., Rees et al. 2002). Furthermore, disturbances of the thalamocortical rhythms characteristic of conscious CNS (central nervous system) states lead to the abolition or alteration of consciousness, as seen in coma, general anesthetics, schizophrenia, and epilepsy (Steriade et al. 1990). Such data need to be accounted for if midbrain structures are to supplant, or to join, the corticothalamic system as the primary candidates for the biological substrate of consciousness.

Consciousness without corticocentrism: Beating an evolutionary path

DOI: 10.1017/S0140525X07000994

David B. Edelman

The Neurosciences Institute, San Diego, CA 92121.
david_edelman@nsi.edu

Abstract: Merker's approach allows the formulation of an evolutionary view of consciousness that abandons a dependence on structural homology – in this case, the presence of a cerebral cortex – in favor of functional concordance. In contrast to Merker, though, I maintain that the emergence of complex, dynamic interactions, such as those which occur between thalamus and cortex, was central to the appearance of consciousness.

In the target article, Merker challenges the pervasive view of the cerebral cortex as necessary for consciousness, and in doing so, beats a path towards a view of consciousness that makes sense from an evolutionary perspective. Merker's arguments are grounded primarily in detailed anatomical and physiological observations, as well as clinical studies and first-hand observations of anencephalic children, and there is a strain in his perspective that is deeply consonant with a modern evolutionary view of nervous system form and function. But he resists the notion that complex inter-areal dynamics in the nervous system were a necessary basis for incipient consciousness. In contrast, I maintain that complex dynamic interactions – such as, but not limited to, those arising in thalamocortical circuitry – were central to the emergence of the conscious process.

Like Merker, I believe that consciousness may not be contingent upon the particular anatomy of the cerebral cortex. The probability that some birds are conscious (see Butler & Cotterill 2006; Edelman et al. 2005) suggests that differently organized brain nuclei, with perhaps less well-defined lamina than mammalian cortex, are up to the task of sensory integration and interaction with thalamic nuclei, thereby yielding conscious states (notwithstanding the suggestion that the avian "wulst" is a cortical homolog, a notion that remains controversial; see Karten 1997). If consciousness emerged independently in the avian and mammalian lines (or in their reptilian, or stem amniote, precursors), it involved the elaboration of quite different structures serving identical functions. The centrencephalic system, *sensu stricto*, may not be necessary for conscious states. Moreover, invertebrate species, such as the cephalopod molluscs, with nervous

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

systems that are radically different in their organization than those of vertebrates, may well have some form of primary consciousness (Mather, in press). Although this idea remains woefully untested, it nevertheless seems clear that neural structures with different evolutionary histories and developmental trajectories may subserve similar functions, including the dynamic interactions underlying conscious states.

In general, biological structures and their particular functions do not emerge entirely *de novo* in the course of evolution. Rather, natural selection shapes, or retrofits, what is already on hand. Hence, although the appearance of a cortical mantle certainly enriched the contents of consciousness, it did not necessarily mark the emergence of incipient consciousness. In a given lineage, a certain function may predate the appearance of a structure which, in members of an extant species, has come to be associated with it. The new, or modified, structure may either have become part of a preexisting "circuit" serving this ancient function or simply co-opted the function entirely. Moreover, structural and functional convergences are not at all rare in the evolutionary histories of complex animals. Given what we can surmise from broadly comparative anatomical studies of present-day species, this seems to have been particularly true during the evolution of the nervous system and its associated sensory modalities. The oft-cited compound eye, which probably appeared a number of times independently in different evolutionary lineages (Oakley & Cunningham 2002; but see Gehring 2005), is an example of the latter.[1] The apparent convergent architectures (i.e., laminar structure) and physiologies (i.e., binocular vision) of the so-called avian wulst and mammalian neocortex (Medina & Reiner, 2004; Reiner et al. 2005) may be an example of the former. Surveying evidence from anatomical, physiological, and behavioral studies, my colleagues and I make precisely this argument in a recent paper (Edelman et al. 2005).

Merker's resurrection and substantive revitalization of Penfield and Jasper's (1954) "centrencephalic" hypothesis provides a novel anti-corticocentric view of consciousness. However, I disagree with his premise that elaboration of complex functional circuitry was not critical for the emergence of consciousness. The centrencephalic system appears to be the site of quite complex dynamic interactions between ascending (or attentional) systems, a relay locus, and integration centers. In two recent papers (Edelman et al. 2005; Seth et al. 2005), my colleagues and I suggest that a *sine qua non* of mammalian consciousness may be the dynamic interaction between thalamus and cortex, an idea first expressed by Edelman and Tononi (2000) in their "dynamic core" hypothesis nearly a decade ago. But, I will allow that, although reentrant thalamocortical loops may be the functional core of mammalian consciousness, theoretically neither cortex and thalamus, nor their underlying architectures, are necessary for conscious states. What consciousness requires, it seems, are richly and reentrantly connected structures that support essentially *the same functional interactions* as thalamus and cortex.

In making the case for consciousness in anencephalic children, Merker cites one published account documenting the assessment of four hydranencephalic children in which the authors conclude that all four children are conscious by the criteria of a standard neurological examination (Shewmon et al. 1999).[2] He also reports his first-hand impressions of the behavior of anencephalic children, as well as observations gleaned from the reports of parents of anencephalic children. Of these observations, perhaps most intriguing are reports that these children have seizures of absence epilepsy. In the case of anencephalic children, though, it is difficult to determine whether these individuals are conscious. Apart from limited behavioral means (obviously, no accurate verbal report is possible), there is little that can be done to test for conscious states. Collectively, Merker's accounts lack the weight of evidence. His anatomical sketch of the connectivity between midbrain structures, including the hypothalamus, periaqueductal gray, and superior colliculus, might suggest a neural substrate fully capable of complex integration of action and motivation, and thus generation of a detailed internal "world" map. Moreover, the absence of vast radial migrations of cortical progenitor cells during neurogenesis (as must be the case in anencephalic embryos) might allow further elaboration of otherwise deeper, subcortical, structures. But these prospects remain unverified and little explored.

The evolutionary implications of conscious states in animals that lack a cerebral cortex are ripe for exploration. Merker has made an intriguing foray into this realm, but much territory remains uncharted; an exciting prospect indeed.

ACKNOWLEDGMENT

Preparation of this commentary was supported by the Neurosciences Research Foundation.

NOTES

1. Interestingly, certain regulatory genes that are important in the specification and patterning of structures such as eyes and, indeed, large portions of nervous systems and whole body plans, are widely conserved across invertebrate and vertebrate taxa. This insight, which emerged shortly after the discovery of the first homeotic, or hox, genes, is all the more tantalizing because the same hox genes expressed in representatives of disparate taxa have often been found to induce tissues of quite different embryonic origins to form functionally homologous structures during development (Carroll et al. 2001).

2. According to Merker, this is "the only published account based upon an assessment ... under near optimal conditions" (target article, sect. 5, para. 4).

Roles of allocortex and centrencephalon in intentionality and consciousness

DOI: 10.1017/S0140525X07001008

Walter J. Freeman

Department of Molecular and Cell Biology, University of California at Berkeley, Berkeley, CA 94720-3206.

dfreeman@berkeley.edu

http://sulcus.berkeley.edu

Abstract: "Decortication" does not distinguish between removing all cerebral cortex, including three-layered allocortex or just six-layered neocortex. Functional decortication, by spreading depression, reversibly suppresses only neocortex, leaving minimal intentionality. Removal of all forebrain structures except a hypothalamic "island" blocks all intentional behaviors, leaving only tropisms. To what extent do Merker's examples retain allocortex, and how might such residues affect his interpretations?

In considering the nature and functions of cerebral cortex, particularly as distinct from cerebellar cortex, it is useful to distinguish between two main categories. Three-layered allocortex (Mountcastle 1974, p. 232) is common to all vertebrate brains. It includes archicortex (hippocampus), paleocortex (prepyriform and periamygdaloid cortices), and the laminated neuropil of the olfactory bulb, though inclusion of the latter as "cortex" is controversial (Braitenberg and & Schüz 1998). Six-layered neocortex is found only in mammals, with transitional forms in marsupials; its well-known variants are distinguished by input-output connections and cytoarchitectures (e.g., Brodmann 1909).

A method for chemical decortication (Bures et al. 1974) relies on inducing the *spreading depression of Leão* to inactivate the cortex in each cerebral hemisphere. Under surgical anesthesia the scalp of the subject, usually a rat, is incised and reflected, and two small burr holes are made through the calvarium. The skin is closed loosely, and the animal is nursed to recover from the anesthetic. Then the skin is momentarily reflected, and a cotton pledget soaked in concentrated potassium chloride is placed over each burr hole. Within a minute or two the potassium

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

induces intense neuronal spiking that releases sufficient potassium ions into the intracortical extracellular space to precipitate a chain reaction that spreads in mm/minute over the entire neocortex in each hemisphere – but not beyond across the entorhinal fissure into the allocortices. The functional decortication lasts several hours and is fully reversible. Bures demonstrated "neodecortication" for me in Prague; on casual inspection I saw surprisingly little difference in the rat's behavior before, during, and after the process.

Phylogenetic evidence for the functions of allocortex stems from analyses of the brains and behaviors of simpler vertebrates, particularly the salamander (Roth 1987) – a neotenic amphibian that C. Judson Herrick (1948) regarded as the closest living descendent of the putative vertebrate ancestor. The three main parts of its forebrain are sensory (predominantly olfactory bulb with anterior olfactory nuclei), motor (pyriform cortex with paleostriatum), and associational (primordial hippocampus with septoamygdaloid nuclei). These components comprising the bulk of the primitive forebrain constitute the limbic system, which suffices to elaborate the goal-directed behaviors on which all vertebrates rely for survival.

The functions of these allocortical parts persist in mammals: most obviously, in support of olfaction, spatial orientation using the "cognitive map" (Jacobs 1994; O'Keefe & Nadel 1978), and temporal orientation in constructing a life history through learning dependent on short-term memory. These integrative processes are essential for intentional action into the world, because even the simplest search for food or shelter requires that an animal coordinate its position in the world and track its trajectory toward its target.

Selective partial removal of allocortex has profound effects on intentional behaviors. The bulbectomized rat provides the best biological model for intractable clinical depression (Jesberger & Richardson 1985; van Riezen & Leonard 1990). Damage to the mesial temporal lobes, which contain substantial parts but not all of the limbic system, results in severe loss of spatial and temporal orientation, compromising but not abolishing intentional behaviors or, apparently, consciousness. In contrast, bilateral destruction of selected areas of neocortex results in catastrophic but delimited losses in sensory and motor functions, including "social blindness" from frontal lobe damage, but not in loss of consciousness. I agree with Merker that the adaptiveness and flexibility of intent, the fullness of life-long memory in the unity of consciousness, and the cognitive contents of consciousness are elaborated by neocortex, but argue further that these three aspects are integrated predominantly in the allocortical limbic system (Freeman 2006), more than in Wilder Penfield's "centrencephalon integrating system" (Penfield & Jasper 1954).

On the one hand, the effects on behavior of full decortication have been studied in great detail for well over a century, beginning with the celebrated study of Friedrich Leopold Goltz (1892) that reportedly stunned his audience. The crucial work of postmortem verification of the extent of tissue removal was entrusted to an independent investigator at the beginning of his illustrious career, Sir Charles Sherrington. I have not seen Sherrington's report to the neurological congress in which Goltz reported his observations, so my question remains unanswered: Did Goltz surgically remove ("decorticate") parts or all of the allocortex or only neocortex, as in functional decortication? On the other hand, the removal of all cortex and striatum, leaving a hypothalamic "island" that is adequate for neurohumoral control (Bard & Rioch 1937) but not temperature regulation (a rectal thermostat, heater, and air conditioner are required for each subject), deprives animals of all intentional behaviors and leaves blind tropism without consciousness (as far as I could tell on my visit to Bard's laboratory). Merker cites Bard but he does not cite the work of Goltz, nor of Bures on spreading depression, nor does he cite the distinction between three-layered allocortex and six-layered neocortex, so I pass the question to him: How much of the olfactory and hippocampal cortices remained in the brains comprising his database?

A brain for all seasons

DOI: 10.1017/S0140525X0700101X

R. Allen Gardner

Department of Psychology and Center for Advanced Studies, University of Nevada, Reno, NV 89557.

gardner@unr.edu

Abstract: Merker's fine article opens a new view of brain function consistent with current developments in robotics, heuristics, and fuzzy logic. A reciprocal, tripartite organization of input/motivation/output in the midbrain can accomplish the practical tasks of a brain. A bold move places consciousness in the midbrain, raising profound questions about the practical nature of consciousness.

This is a fine article. It opens up a new way to view how brains work. It converges on current developments in robotics, heuristics, and fuzzy logic. As in Brooks' (1986; 1989; 1990; 1991) subsumption architecture, duly noted in this target article, Merker here shows that reciprocal, tripartite organization of input/motivation/output can accomplish the practical tasks of a brain. In this inspiring view, sensory cortex feeds information to midbrain, and midbrain allocates motor resources, and all three act and interact in real time. Merker outlines a reciprocal inside-out/outside-in organization as opposed to the traditional, intractable opposition between top-down and bottom-up. He shows how human neocortex, which is also higher, relative to gravity, can emerge from evolution of more and more powerful sensory, motor, associative, and computational functions, rather than more and more complex executive functions.

In modern times, robots accomplish more and more practical tasks without consciousness. I am among hundreds of thousands of satisfied owners of a relatively inexpensive robot that vacuums floors – backing away from obstacles, following walls, sensing relatively dirty areas for more intensive cleaning, sensing when its battery needs recharging so it needs to stop vacuuming and seek a recharging station. A more advanced model senses proper time to leave its recharging station to start a fresh round of vacuuming. Future models could grease their own bearings or chase away intruders. In a tripartite system such as Merker's, or a subsumption system such as Brooks's, functionality could be added by increasing motor, sensory, and computational capacity in an analogue of the cerebral cortex. The only practical limits would be cost and consumer demand.

Traditionally, both animals in fields and self-interested humans in marketplaces calculate relevant information to arrive at optimal courses of action. In modern times, Gigerenzer et al. (1999, pp. pp. 1–118) and Todd and Gigerenzer (2000) point out that players in field and marketplace rarely, probably never, have access to enough information to arrive at optimal decisions. Moreover, successful action must be prompt action. Prompt action cannot wait to acquire and calculate sufficient information to arrive at an optimum. Gigerenzer and Todd show how players in field and marketplace can take advantage of what they call "fast and frugal" heuristics to arrive at less than optimal, but still useful, decisions.

In field and marketplace, players must divide limited resources among conflicting, often critical, needs. Once again, practical limits of information and time preclude optimal solutions. Meanwhile, fuzzy logic systems, introduced by Zadeh and Kacprzyk (1992), described by Kosko (1993), and applied to industrial and biological examples by Kipersztok and Patterson (1995) and Gardner and Gardner (1998), offer fast and frugal, and

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

most important, effective and profitable, solutions to problems of apportioning limited resources among conflicting needs.

Erickson (1984) and Erickson et al. (1994) show how modern accounts of color vision can generate the entire visible spectrum with three or only a handful of receptor types, each tuned to a particular wavelength, but each with a band of decreasing sensitivity that overlaps with the others. Erickson (1984) and Erickson et al. (1994) show how this system of relatively few receptors reappears in other modalities. Erickson (1984) also shows how this system of few tuned elements with overlapping bands of sensitivity applies to modern findings of motor systems. Each color, visual angle, taste, and so on, in such systems has a unique code based on the output of a population of receptors. Likewise, each movement in space has a unique code based on a population of afferent outputs. Consequently, efferent and afferent systems can communicate directly and effectively without wasteful intermediary centers. This relieves a midbrain system, such as Merker's, from the burden of centers that must read inputs, translate, and then write outputs, thereby freeing the system to allocate resources among biological needs that realistically fluctuate from moment to moment.

Merker locates consciousness in the midbrain. This is a bold move that raises profound questions about the nature of consciousness. Locating consciousness in a specific structure endows consciousness with a reality that it seldom possesses in cognitive theories. This move faces questions about deciding where, in palpable anatomy, consciousness resides in the brain. This move also faces questions about deciding which beings can exhibit consciousness and which cannot. Brooks and Brazeal (see Brooks 2002, Ch. 8) have raised this question with the robot Kismet with unsettling results. It remains to be seen whether Merker and the parents of infants with cortical birth defects can answer skeptics with firm conviction and subjective observation alone.

Cognitive achievements with a miniature brain: The lesson of jumping spiders

DOI: 10.1017/S0140525X07001021

Emmanuel Gilissen

Royal Museum for Central Africa, Department of African Zoology, 3080 Tervuren, and Université Libre de Bruxelles, Laboratory of Histology and Neuropathology, 1070 Brussels, Belgium.

Emmanuel.Gilissen@africamuseum.be

Abstract: The observation that an animal's behavior is largely unaltered even after profound modifications of sizeable brain portions, suggests a large flexibility in the relationships between species-specific brain structures and species-specific behavior. In this perspective, a fascinating example is given by the comparison of jumping spiders and felids, where similar predatory behaviors are achieved with totally different brain substrates.

The conscious mode of functioning is conceived in the target article as being dependent on specific neural arrangements rather than as being the result of a general increase in informational capacity or complexity achieved by expansion of a structural substrate. This view is in sharp contrast with possible conclusions from studies on self-recognition in mammals. When tested among primates for example, self-recognition – a case of conscious mode of functioning – is observed in great apes and humans, but not in monkeys (Anderson 2001). Among other mammals only large brained cetaceans recognize themselves in a mirror. This capability of self-recognition can be seen as an example of psychological evolutionary convergence with great apes and humans (Delfour & Marten 2001; Reiss & Marino 2001; but see Manger 2006). Moreover, considering that there may be at least a bias for the processing of "self" within the human right prefrontal cortex (Keenan et al. 2000) – a cortical region that, on the basis of examination of the cytoarchitecture, is either absent or very small in cetaceans (Manger 2006) – it could also be argued that self-recognition is a by-product of brain size increase and could indeed be considered as the result of a general increase in informational capacity achieved by expansion of the brain, which below a certain absolute volume does not support self-recognition (see also mirror self-recognition experiments in elephants; Povinelli 1989; Plotnik et al. 2006). This conclusion is somewhat nested in the statement of Merker when he defines reflective awareness as more akin to "a luxury of consciousness on the part of certain big-brained species, and not its defining property" (sect. 1, para. 5). Hence, the definition of consciousness as conceived in the target article is restricted to the state of wakefulness and responsiveness wherein mostly brainstem structures are necessary.

In the framework of this definition, the observation that the behavior of decorticated rats or cats remains from all viewpoints largely the behavior of a rat or of a cat with almost intact cognitive capabilities raises another important issue. Considered from a comparative viewpoint, the various specific behaviors of animals could be understood as adaptative responses of different organisms to dynamic eco-physiological demands. It remains an open research subject to elucidate how specific adaptative behaviors are anchored in specific brains. In other words, is cat brain the only kind of brain that can sustain cat behavior? To what extent does it differ from horse brain, which would be the only brain adequate to sustain horse behavior? The analysis of Merker shows that the competences of decorticate animals reflects the capacity of upper brainstem mechanisms to sustain the behavior required by the adaptations of their species. The fact that this behavior is largely unaltered even after profound alterations of large brain portions suggests a huge flexibility in the relationships between species-specific brain structures and species-specific behavior.

In this perspective, a fascinating example is given by the comparison of jumping spiders and felids. Few terrestrial arthropods catch active prey by stalking them, in the manner of mammalian carnivores. One arthropod group, however, the jumping spiders (*Salticidae*), adopts a strategy in catching prey that is sufficiently similar to that of a cat catching a bird, that is, to creep toward the prey until the chance of escape is small and then spring on the prey. Catching a fly or another spider by stalking is in principle not very different from catching a mouse or a bird. Hence, jumping spiders have evolved a range of visual mechanisms that are remarkably similar to those of predatory higher vertebrates, including complex pattern recognition capabilities. The salticid genus *Portia*, for instance, includes African, Asian, and Australian species that all exhibit complex predatory strategies. *Portia*'s preferred prey is other spiders. The capture of this prey involves behavioral sequences based on performing aggressive-mimicry web signals, problem solving, as well as planning. Flexibility in *Portia*'s predatory strategy clearly characterizes navigation, for which the detouring behavior is particularly illustrative.

Portia routinely reaches prey by taking indirect routes (detours) when direct paths are not available. This even includes detours that require movements initially away from the prey, where the prey is temporarily out of view, or detours and approaches from the rear, when safer, even when direct routes are available (Tarsitano & Andrew 1999). Lions have been observed making such comparable detours when hunting their prey (Schaller 1972). The taking of detours by lions has not been studied experimentally. It can nevertheless be reasonably interpreted as "planning ahead" behavior. The point here is that *Portia*, despite operating with a miniature nervous system, adopts a predatory strategy similar to the one of a lion.

Such an issue is far from trivial. The predatory strategies of *Portia* imply that its visuospatial acuity is more similar to that

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

of a mammal than to that of an insect, although the size difference is enormous. There are more than 150 million photocells in the human retina, but in a *Portia*'s eye, the photocells number only in the thousands. It is the design of the eight eyes, especially the pair of large forward-facing antero-medial (or "principal") eyes (Figs. 1 and 2), which are responsible for *Portia*'s acute vision (Harland & Jackson 2000). Jumping spiders are not cats however, and their behavioral repertoire for catching prey shows limitations when compared to mammals. A big difference between *Portia* and cats appears to be the speed at which problems are solved. Nevertheless, these limitations only become clearly apparent when the spider is taken out of the natural situation to which it is adapted and made to perform tasks in a laboratory setting. On the other hand, these behavioral limitations are accompanied by an extraordinary degree of neural economy. Arthropods indeed have single cells performing functions that require tens or hundreds in higher vertebrates (Land 1974). More specifically, a salticid spider such as *Portia* makes efficient use of its limited resources for seeing and overcomes many (but not all) of the constraints imposed by its small size. It then is able to achieve considerable cognitive skills, such as problem solving and planning ahead.

In the context of the theoretical implications of the target article, it is of prime interest to know that an animal whose neural machinery is characterized by such a degree of economy also exhibits activities so strikingly similar to those of a mammal.



Figure 1 (Gilissen). *Portia africana*. Size range: 8 to 12 mm. Courtesy Rudy Jocqué.

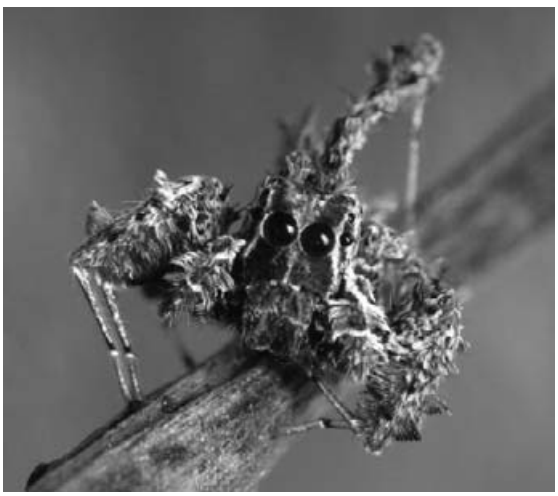


Figure 2 (Gilissen). *Portia fimbriata*. Size range: 8 to 12 mm. Courtesy Sudhikumar Ambalaparambil.

ACKNOWLEDGMENTS

I thank Rudy Jocqué (Royal Museum for Central Africa, Tervuren, Belgium) who introduced me to the world of *Portia* and who provided the illustrations presented here as well as helpful comments on the text.

I Promethean, bound deeply and fluidly among the brain's associative robotic networks

DOI: 10.1017/S0140525X07001033

Robert B. Glassman

Department of Psychology, Lake Forest College, Lake Forest, IL 60045.
glassman@lakeforest.edu
http://campus.lakeforest.edu/~glassman/

Abstract: Merker's insightful broad review fertilely recasts the mind/brain issue, but the phenomenological appeals require additional considerations of behavioral and neural flexibility. Motor equivalences and perceptual constancies may be cortical contributions to a "robotic" tectal orientation mechanism. Intermediate "third layers" of associative neural networks, each with a few diffusely summing convergence-divergence modules, may be the economical expedient by which evolution has extended the limited unity-in-diversity of sensorimotor coordination to perception, action, thinking, and memory.

"*I hope to share with you my fascination with consciousness. Each of you is unique in being at the center of your own awareness, reaching out to the world and other individuals and the stars*." I begin my biopsychology courses thus inviting awe; then explore the subject of consciousness with student colleagues (Glassman 2002). In 2007 we will read Bjorn Merker's extraordinary synthesis correlating phenomenological consciousness with brain architecture.

Empathy is not enough. Are parts of the article "just-so stories" that conveniently select anatomical or behavioral facts? The first and last sections are fragile in their appeals to empathy, among these, the tormenting ethical "dividing line" issues associated with the touching description of conscious anencephalic children. Are physicians who describe these patients as "vegetative" (sect. 5) attempting a virtuous authoritative role by invoking a mythology to frame pained decisions not to exhaustively engage life-support technology?

We who have even tiny-brained pets like parakeets or goldfish hardly doubt they are conscious. Their behaviors include analogies with anencephalic children's, such as caretaker recognition. Eye-contact empathy occurs especially with anthropomorphic front-eyed pets (Morris 1967, pp. 224–31). Considering Merker's explanation of extreme visual impairment in anencephalic children, his selected Figure 9 photo suggests sham eye-contact based on hearing, as in affectional expressions of children born blind (Eibl-Eibesfeldt 1975, p. 450, Fig. 18.5). Bear in mind that we display related caretaker emotional reactions to dolls and, recently, to high-tech movie animations' uncanny simulations of human facial dynamics, as in Warner Brothers' 2006 film "Happy Feet."

The fact that conscious continuity persisted during Penfield and Jasper's extensive cortical ablations (Penfield & Jasper 1954), says little about localization of consciousness, considering the possibility of rapid compensation or cortical redundancy (e.g., Beach et al. 1960; Glassman & Smith 1988). Analogously, little Parkinsonian deficit may appear until loss of 80% of striatal dopamine terminals (Bezard et al. 2001). Merker's cited instances of absence epilepsy with seizures might be due to loss of tonic arousal rather than a loss of centrencephalic organization.

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Visual evolution leads, but "robotic" sensorimotororienting is not enough. Merker argues that mobile visual organization led neurocognitive evolution, with the growing faciliness of adaptive recalibrations among topographic sensory mappings. This compelling thesis about the emergence of an *ego center*, around which individuals maintain their own postures in a flux-ridden world, complements the good perspectives of Donald T. Campbell and of Richard Gregory, that evolution of vision became tantamount to *knowing* and *planning*, in freeing organisms to respond to distal stimuli. Vision was the seed for the natural selection of ability to reach deeply into one's past, future, and spatial environment, to "look ahead." Scientists' hypothesis testing, using symbolic thought, evolves naturally from our routine "testing of object hypotheses" in distal perception (Campbell 1956, 1966, 1974; Gregory 1970, 1978).

The spatiotemporal problem of bodily orientation is "intermediate in complexity." More neural machinery is needed to carry it off well than for a segmental reflex, yet enough room for that machinery resides in the narrow hallway of the mesodiencephalon. Yes, there is intriguing *unity-in-diversity* in organisms' ability to orient toward any place within their spheres, but there is also a dull sameness about orienting responses.

Motor equivalence (Milner 1970) and *perceptual constancies* (Rock 1995) comprise more interesting forms of *unity-in-diversity* and more varied, complex relationships between organism and environment – suggestive of consciousness. Such organismic competencies in mediating *patterns* of perception and action have proven most difficult to computerize, like the persistent failure to create a speech machine that emulates ordinary human conversational competence well enough to pass the Turing test (Shieber 2004). Industrial robot arms' graceful orientational movements remain "robotic" in their stereotyped repetitiousness; they achieve organismic flexibility only when teleoperated by a human. Merker may be making a localist error, in placing consciousness in the mesodiencephalic orientation robot, instead of in the larger emergent system.

During the 1960s, watching my advisor, James Sprague (see sect. 3.1) carry out his elegant neurological tests inspired me. In my own later experiments, orientation toward appetitive stimuli sometimes displayed a robotic character, even when visual, auditory, or tactile localizing stimuli could substitute for each other – in cats better than rats (Glassman 1970, 1994). Further evidence that appetitive orientation does not necessarily involve consciousness is in "blindsight" (Weiskrantz 2004). In agreement with some of Merker's points about spherical coordinates (sects. 4.3 and 4.5), an unusual degraded "robotic" orientation response, with dissociated pitch and yaw, appeared during early postoperative days in some cats having large cortical ablations (Glassman 1983). For example, sometimes when a food morsel touched the forepaw of the blindfolded cat, there was first a vertical movement of the snout down to the level of the paw and then a sluggish horizontal turn toward the stimulus side.

Economical connectivity may increase behavioral flexibility. What underlying organization does that "seam" suggest? Sensorimotor behavior normally displays beautiful continuity. An input-output system having few dimensions might save connectivity via data reduction to an intermediate layer of diffusely excitable modules having convergent inputs and divergent outputs. For example, a two-layer network of direct connections between a mosaic of $s = 1000$ distinguishable skin patches and $r = 100$ independently controllable muscle units, requires $sr = 100{,}000$ weighted connections to accurately orient a movement. With an intermediate layer having three summators to integrate input-output associations for three spatial dimensions, $3s + 3r = 3300$ connections suffice (Glassman 1985). The sandwiched associative layer also enhances plasticity, because reciprocal coordinated adjustments in synaptic weights need occur only among the connections of the three modules.

Similar considerations apply to superimposed topographically organized inhibitory circuitry; Merker discusses the economy of such connectivity of the zona incerta (sect. 4.5, Fig. 7). Inhibition can be more diffuse than excitation because damping down responsiveness is inherently less demanding than is achieving accurate threshold, timing, and directionality of an active response. Hence, inhibitory mapping requires less resolution to achieve comprehensive competitive overlap. This yields a safety-factor bonus. Diffuse inhibition makes inaction the default condition, like a "dead man's handle"; foci of excitation have to "break through." A danger in symmetrical "design" of excitatory and inhibitory mappings is that mismatch errors might allow leakage of fragmentary excitation foci, for example, as misplaced sensations, or dyskinesias.

Consciousness in memory extends sensorimotor action organization. Analogous savings considerations might apply to the discussion in section 4.5.2 of cortical long-term memory economy, although most attributes of memory are not literally spatial "dimensions." That is, when a species repeatedly encounters a particular *qualium*, the ability to deftly handle variations of that attribute of its world might evolve more readily if its neural representation were to reify as an independent module, with its own connectivity convergences and divergences. Is *this* what that vast memo-sheet of cortex contains?

In each moment of consciousness immense long-term memory donates a few chunks to working memory (sects. 4.1 and 4.5.2), whose bottlenecked small capacity is robustly similar across species, time scales, and experiential contexts. Small working memory may be a "design factor" limiting combinatorial "explosiveness" (Glassman 1999, 2003); an "ego center" can handle just so much at once. Merker's insight, that the concentration of vertebrate motor outputs caudal to the mesodiencephalon implies that the neural nexus for consciousness is located there, ought to be qualified by noting that we are often quietly thinking. Yet, combinatorial logic must also apply to "cognitive actions." Therefore, evolution of higher cognition may indeed branch from the same slender trunk as has served primitive vertebrates' action-organization.

This wonderfully fertile article has added much to my "to-read" list.

Levels of emotion and levels of consciousness

DOI: 10.1017/S0140525X07001045

Carroll Izard

Department of Psychology, University of Delaware, Newark, DE 19716.
izard@udel.edu

Abstract: Merker makes a strong case for the upper brain stem as being the neural home of primary or phenomenal consciousness. Though less emphasized, he makes an equally strong and empirically supported argument for the critical role of the mesodiencephalon in basic emotion processes. His evidence and argument on the functions of brainstem systems in primary consciousness and basic emotion processes present a strong challenge to prevailing assumptions about the primacy of cognition in emotion-cognition-behavior relations.

The central proposition in this commentary is that basic emotions constitute the motivational system ("bias") in the processes of primary consciousness. To relate Merker's conclusion that the mesodiencephalon processes the essential attributes of primary or phenomenal consciousness to compatible emotion theory and research, I will identify two developmental levels or types of emotion and relate them to two levels of consciousness.

Evidence suggests that the mesodiencephalic neural arrangement identified by Merker, through reciprocal connections with other subcortical systems (e.g., amygdala), generate basic

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

emotion expressions and feelings that play a critical role in organizing primary consciousness and motivating its constituent processes. Basic emotion processes in primary consciousness may help explain the behavior currently attributed to the "new unconscious" (cf. Hassin et al. 2005) and to the "perception-behavior link" (Chartrand et al. 2005).

Emotion schemas. An emotion schema (e.g., love, jealousy, interest in science) represents a dynamic interaction between an emotion and associated perceptions, appraisals, and thought. Emotion schemas emerge in synchrony with cognitive development, and some of them (e.g., shame, guilt) are dependent on a concept of self and on relationships with others (Abe & Izard 1999).

Basic emotions. Basic emotions like joy, sadness, anger, and fear are considered as natural kinds, products of evolution that have a common and universal set of components (neural, bodily/expressive, feeling, action tendency) and characteristics (motivational and regulatory functions) (Izard 2002, 2007 cf. Panksepp 2005b). They can be activated by sensory detection or simple perception of an ecologically valid stimulus and do not require conceptual thought (Ohman 2005). Once activated, they become motivational/functional and regulatory (in terms of target selection and action selection) via rapid, automatic, subcortical information processing, independent of neocortical activity (LeDoux 1996). Thus, they have the characteristics to fulfill the role of the "motivational bias" that Merker identifies in the target selection – action selection sequence mediated by the mesodiencephalic system that supports primary consciousness. The basic emotion of interest is of special significance here. It can be activated by any non-aversive change in the sensory fields, has the capacity to drive and regulate attention and information processing (Lundqvist & Ohman 2005; Silvia 2006), and is critical in the organization of conscious processes and in establishing and maintaining interaction with the social and physical environment (Izard 2007).

Merker's evidence and analysis relating to the brainstem system of primary consciousness indicates that basic positive and negative emotions are well within the purview of children without a cerebral cortex. He identifies expressive behavior patterns in these children that characterize the basic emotions of interest-excitement, joy, and anger in normal infants and young children (cf. Izard et al. 1995).

Levels of consciousness. There is considerable agreement that there is a clear distinction between reflective and primary consciousness (Block 2005; Chalmers 1996; Edelman 2006; Morin 2006; Rosenthal 2002). Reflective consciousness is characterized by symbolic processes, memory, and, ultimately, the capacity for awareness of self and others and for monitoring one's own behavior. As Merker convincingly demonstrates, primary consciousness is characterized by sensory processes that generate subjective feelings (cf. James 1890/1950; Izard 1990), especially emotion feelings, and also includes awareness of and responsiveness to objects in the environment. Apparently, processes in primary consciousness are also critical in early development of normal infants' emotion-expressive/social-communicative behavior that facilitates the forming of social bonds and a network for social support (Shiller et al. 1986; Termine & Izard 1988).

Primary consciousness in normal young infants. The mental processes, particularly the emotion processes, of normal young infants probably operate in primary consciousness, supported by the mesodiencephalon in interaction with the amygdala and hypothalamus. Their cerebral cortex is quite immature and its connections to brainstem systems are still rapidly developing (Bauer 2006; Greenough 1991; Posner & Rothbart 2000). Nevertheless, 3-day-old infants can discriminate their mother's voice and work to produce it (DeCasper & Fifer 1980). Three- to 4-month-old infants can form concepts, (Quinn et al. 2001), and 6-month-old infants can form associations between memory representations that are absent (Cuevas et al. 2006). Of course, young infants (0–9 months) are incapable of long-term memory, higher-order cognition, and self-awareness (Bauer 2006; Lewis et al. 1983), and hence cannot engage in the processes of reflective consciousness.

Emotion processes in primary consciousness. From a developmental perspective, it is expectable that emotion expressions and behavioral activities of normal young infants would be similar to those of children without a cerebral cortex. The effects of the emotion expressive behavior of these contrasting groups of children have similar effects on parents and enhance the development of meaningful parent-child relationships. A child without a cortex cannot regulate emotions efficiently or exercise cognitive control of emotion-expression or emotion-related behavior. The same is true of normal young infants. They depend almost entirely on non-cognitive processes for soothing or regulation of intense/run-away emotions following the acute pain of inoculation (Izard et al. 1987).

Emotion prowess in primary consciousness. Four-month-old infants can discriminate and respond differentially to discrete positive and negative emotion expressions of their mothers (Montague & Walker-Andrews 2001), an ability that will eventually facilitate empathic responding. Even 3-month-old infants often take the initiative in displaying and responding with emotion when their mother makes a poker face and remains still and silent (Hembree 1986; Tronick & Cohn 1989). Such expressive-behavior play is fundamental to the development of emotion knowledge (the understanding of the expressions, feelings, and functions of emotions) that will eventually become critical to the development of interpersonal skills and the prevention of psychopathology (Denham & Burton 2003; Izard 2002).

Emotion processes in primary consciousness in adults. Evidence suggests that a brainstem-amygdala network mediates the activation and expression of basic emotions in human adults (Ohman 2005). The behaviors facilitated by brainstem mechanisms in primary consciousness may bear some similarity to behavior currently attributed to "nonconscious" or "unconscious" cognitive and emotional processes in normal adults.

It is speculative to compare psychology's "new unconscious" (Hassin et al. 2005) and "perception-action link" (Chartrand et al. 2005) with processes in primary consciousness (Block 2005; Edelman 2006). Nevertheless, they clearly have a central feature in common: they both involve unreportable mental processes (including emotion processes) that affect behavior. Processes mediated by brainstem or brainstem-amygdala circuits generate "unconscious" emotion feelings that affect behavior in observable ways (Ohman 2005; Winkielman & Berridge 2004). Attributing causal roles to emotion processes in primary consciousness may be more straightforward and more heuristic than attributing causal roles to the "unconscious" and particularly to "unconscious emotions."

Concluding remarks. The term primary or phenomenal consciousness as defined by Merker and others may provide a better descriptor for some of the processes currently attributed to the "unconscious," and particularly to "unconscious emotion" (cf. Panksepp 1998a). Attributing emotion feeling to primary consciousness means that one can become conscious of a feeling that one cannot label and articulate (cf. Bruner et al. 1956), as demonstrated in normal infants and children without a cerebral cortex, and hypothesized to be the case for anyone (Izard 1991).

The tendency in psychology has been to assume that mental processes operate either in reflective consciousness or in an "unconscious domain," neither of which explicitly correspond to or adequately frame the processes of primary consciousness described by Merker and a number of philosophers and scientist-philosophers (e.g., Block 2005; Edelman 2006; Rosenthal

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

2002). Lack of a clear differentiation among processes in primary consciousness and in other levels of mental functioning may add to confusion and slow the development of scientific interest in the subject. Merker's target article presents a strong challenge to the prevailing notion of cognitive primacy in emotion processes and in emotion-cognition-behavior-relations (cf. Zajonc 1980).

ACKNOWLEDGMENTS

Preparation of this article benefited from the support of NIMH grant #R21 MH068443, conversations with Paul Quinn, and the assistance of Fran Haskins.

Target selection, attention, and the superior colliculus

DOI: 10.1017/S0140525X07001057

Richard J. Krauzlis

Salk Institute for Biological Studies, Systems Neurobiology Laboratory, La Jolla, CA 92037-1099.

rich@salk.edu **http://www.snl-k.salk.edu/**

Abstract: Consistent with the target article, recent evidence indicates that the superior colliculus (SC) is somehow involved in target selection. However, it is not yet known whether this function is inherent to the SC or inherited from its inputs, how the selection process occurs for different movements, or how target selection by the SC is related to covert selection (i.e., attention).

It has been recognized for some time that the intermediate and deep layers of the superior colliculus (SC) in primates plays some role in target selection, at least for saccadic eye movements. For example, the preparation of saccades is correlated with increases in the activity of SC neurons that can begin hundreds of milliseconds before any movement and this activity appears to play a role in representing possible targets (Glimcher & Sparks 1992). Changing the probability that a visual stimulus will be the target – for example, by adding a variable number of irrelevant stimuli – changes the visual and tonic activity of many SC neurons (Basso & Wurtz 1997; Dorris & Munoz 1998). When the subject must search for a uniquely colored target stimulus amidst other colored distracters, many SC neurons discriminate the target from the distracter with a delay that is time-locked to stimulus onset, rather than saccade onset, suggesting that they play a role in target selection in addition to saccade preparation (McPeek & Keller 2002).

Perhaps the most compelling evidence for a role of the SC in target selection, as distinguished from saccade selection, comes from studies of the other type of voluntary eye movement made by primates – smooth pursuit. The SC has long been known to contain a motor map for saccades, but more recent studies have shown that the activity of many saccade-related SC neurons is also modulated during pursuit eye movements. These neurons show a somewhat complicated temporal pattern of activity during pursuit – and also fixation – but this pattern can be explained fairly simply by considering the location of the tracked target within the neurons' retinotopically organized response fields (Krauzlis et al. 1997, 2000). The distribution of activity across the SC motor map therefore appears to provide a real-time estimate of the position of the target in oculocentric or retinotopic coordinates, not restricted to saccades but for orienting movements in general. This "target position map" hypothesis provides what we consider to be a parsimonious alternative to the widely discussed "fixation zone/saccade zone" hypothesis (Munoz & Fecteau 2002), but the issue remains controversial.

The activity of many SC neurons also predicts the subject's choice of target for pursuit as well as for saccades. During a visual search task, many SC neurons exhibit a preference for the target stimulus over irrelevant distracters that emerges over the course of ~100 ms prior to the initiation of pursuit and saccades (Krauzlis & Dill 2002). By interpreting the preference for the target stimulus as a "decision signal," we showed that SC activity could account for the target choices made by pursuit and saccades. We also inferred that pursuit uses a less stringent decision criterion than saccades, perhaps because errant saccades are more costly in their disruption to vision than mistakes by pursuit. These physiology results have been recently corroborated by behavioral studies in human subjects showing evidence that pursuit and saccade choices are guided by a common decision signal, and that the decision to trigger pursuit involves a threshold that is generally lower that that for saccades (Liston & Krauzlis 2003; 2005). The idea of a common decision signal is consistent with the integrative viewpoint put forward in the target article, but these issues are also not yet settled. For example, an alternative viewpoint is that target selection involves a serial linkage between saccades and pursuit, with pursuit simply adopting the choice made by the saccade system (Gardner & Lisberger 2002).

A pair of studies has recently demonstrated the idea that the SC is causally involved in target selection. The first study, focusing on saccadic eye movements, used a visual search task and found that when the region of the SC representing the target was focally inactivated, saccades were often misdirected to distracters appearing in unaffected areas of the visual field (McPeek & Keller 2004). The second study examined both saccades and pursuit using a luminance discrimination task and found that subthreshold microstimulation of the SC biased the selection of targets toward the stimulated location for both types of eye movements (Carello & Krauzlis 2004). The results for pursuit were especially revealing. Because the targets for pursuit initially appeared at a location opposite to its direction of motion, the experiment was able to distinguish between effects on the motor commands (i.e., which direction to move) and effects on the position of the target (i.e., which stimulus to follow). The results showed that altering SC activity changed which stimulus was chosen, regardless of the type or direction of eye movement that was needed to acquire the target. These experimental results provide strong support for the interpretation put forward in the target article that the primate SC plays an integrative role in target selection and decision-making, beyond its conventional role in the motor control of saccades.

What remains unclear from these studies is the extent to which target selection is a function that is inherent to the superior colliculus, a point that is central to the "mesodiencephalic" theory of consciousness put forward in the target article. A fairly common view of these recent findings is that the SC functions as a conduit for selection signals that are generated in other places, such as the cerebral cortex. Unfortunately for the theory, it is difficult to rule out this interpretation, because the extensive cortical and subcortical network involved in target selection makes it difficult to isolate the contribution of individual brain regions. Nonetheless, one crucial test is to determine how the inactivation of various cortical areas involved in target selection alters the properties of neurons elsewhere in the network, including the SC. These experiments would most likely identify multiple sources of support for target selection, but they might also help identify how the basic form of target selection putatively accomplished by the SC is extended in functional scope by the addition of signals from the forebrain.

A better test of the theory is suggested by the strongest prediction put forward in the article, namely that "*one conscious content will not be replaced by another without involvement of the mesodiencephalic system (centered on the superior colliculus) as outlined here, even when that change is unaccompanied by eye movements*" (sect. 4.5.1, para. 4, emphasis in original). Testing the contents of consciousness in animal subjects poses serious

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

challenges, but some recent studies have shown that stimulation in the SC alters performance in ways that mimic visual attention (Cavanaugh & Wurtz 2004; Muller et al. 2005). It is premature to conclude from this evidence that the SC plays a causal role in determining the contents of perceptual awareness, first because "attention" is not synonymous with "awareness," but also because the effects of the stimulation likely extend to a network of areas connected to the SC, including several cortical areas that are themselves implicated in the control of attention. However, similar tests of visual attention can be conducted using selective inactivation of SC neurons, as has been done for target selection. Such experiments would provide an important test of the "mesodiencephalic" theory, and indicate whether further tests seem worthwhile.

In summary, the target article presents a provocative and contrarian theory of consciousness, but one that is supported by recent experimental findings about the role of the primates SC in target selection. Even more importantly, the theory makes specific predictions about the role of the SC in the control of perceptual awareness that could be tested experimentally.

Consciousness is more than wakefulness

DOI: 10.1017/S0140525X07001069

Alain Morin

Department of Behavioral Sciences, Mount Royal College, Calgary, Alberta, T3E 6K6 Canada.

amorin@mtroyal.ca **http://www2.mtroyal.ab.ca/~amorin/**

Abstract: Merker's definition of consciousness excludes self-reflective thought, making his proposal for decorticate consciousness not particularly ground-breaking. He suggests that brainstem sites are neglected in current theories of consciousness. This is so because broader definitions of consciousness are used. Split-brain data show that the cortex is important for full-blown consciousness; also, behaviors exhibited by hydranencephaly patients and decorticated rats do not seem to require reflective consciousness.

In the target article Merker wisely starts by explaining what his view of consciousness is. He defines consciousness as "a state of wakefulness . . . which typically involves seeing, hearing, feeling, or other kinds of experience" (sect. 1, para. 1) but excludes reflective awareness (i.e., being "aware that one is seeing, hearing, and so forth"; sect. 1, para. 6). As such, consciousness is equated with wakefulness and responsiveness to one's environment, and the reader is indeed tempted to concur with the author that consciousness results from activity of subcortical and brainstem mechanisms. In other words, the proposal that consciousness, as defined here, is possible without a cortex does not seem particularly ground-breaking and has been supported by neurophysiological evidence for quite some time now (as Merker extensively documents in the target article).

Merker states that "Few cognitivists or neuroscientists would today object to the assertion that 'cortex is the organ of consciousness'" (sect. 1, para. 7). "With some notable exceptions [. . .], brainstem mechanisms have not figured prominently in the upsurge of interest in the nature and organization of consciousness that was ushered in with cognitivism in psychology and neuroscience" (sect. 1, para. 7). This is not surprising, since what most researchers today are interested in is not "consciousness in its most basic and general sense, that is, as the state or condition presupposed by any experience whatsoever" (sect. 1, para. 2), but in full-blown introspective consciousness – which *does* depend on cortical activity. More than forty-five years of split-brain research has convincingly shown that surgically isolating the cerebral hemispheres alters consciousness (Gazzaniga 2005). At least six main interpretations of commisurrotomy have been put forward (Morin 2001) – of which only one suggests that consciousness is unaltered by the surgical procedure; the other five views (pre- and post-operation dual consciousness, equal and unequal division of consciousness, and dual personhood in the intact brain) all ascribe a key role to the cerebral hemispheres (and thus to the cortex) in consciousness. The fact that Merker does not mention this large body of work in the target article is rather disconcerting.

Hydranencephaly is used by the author to support his view of decorticate consciousness. He reports his first-hand experience with children afflicted by this condition and proposes that "These children are not only awake and often alert, but show responsiveness to their surroundings in the form of emotional or orienting reactions to environmental events" (sect. 5, para. 6). This is followed by a description of behaviors that these children can engage in, including expressing pleasure and aversion, differentially responding to the voice of familiars, showing preferences for situations, and taking behavioral initiatives. It is further observed that decorticated rats can "stand, rear, climb, hang from bars, and sleep with normal postures" (sect. 4.4, para. 2). They can also swim, eat, mate, and defend themselves. The question, of course, is: How should one interpret such behaviors in relation to consciousness? Does expressing emotions or swimming entail "consciousness" as defined by Merker? Certainly. Do these behaviors necessitate self-awareness? Most probably not. This represents a challenge reminiscent of the one primatologists face when trying to determine if apes possess Theory-of-Mind, autonoetic, or metacognitive abilities (see Terrace & Metcalfe 2005). For instance, one can ask animals to recall food locations or past personal events to test autonoetic consciousness. Monkeys can indeed exhibit such behaviors (Menzel 2005; Schwartz 2005), but again, the point is that such behaviors most likely imply wakefulness and responsiveness, but not reflective consciousness.

Merker cites Baars (1988), Mandler (1975), and Miller (1986) as examples of theorists who do not focus on subcortical brain areas in their attempts to explain consciousness. The reason for this is simple: their definition of consciousness is much broader than the one proposed in the target article. To illustrate, Baars' definition of consciousness (1988) includes one's private experience of reading a word, remembering what one had for breakfast yesterday, and the feeling of a toothache – that is, instances of visual and auditory images, inner speech, bodily feelings, and so forth. Consciousness also contains "peripheral" information at the fringe of conscious experience – for example, the vague awareness one has of surrounding noises. Consciousness also encompases one's access to current beliefs, intentions, meanings, knowledge, and expectations, as well as voluntary control. Baars' more operational definition of consciousness requires that (1) the organism can testify that it was conscious of something following the conscious experience, and (2) an independent effort at verifying the accuracy of the experience reported by the organism be made. Interestingly, Baars rightly notes that in reporting its experience the organism engages in a metacognitive act. Clearly, such a view of consciousness goes far beyond wakefulness and incorporates autonoetic consciousness (access to one's autobiography and mental time travel), self-description, verbal report, metacognition, and self-agency. These various facets of consciousness are reflective in essence.

If one defines consciousness simply as a state of wakefulness and responsiveness, then of course only brainstem sites are necessary, and Merker's careful analysis is very useful in that respect. However, if one embraces the more common view of consciousness which includes self-reflection (e.g., Dennett 1991; Schooler 2002; Zelazo 1999), then obviously cortical areas are involved (e.g., Craik et al. 1999; Goldberg et al. 2006; Johnson et al. 2002; Kjaer et al. 2002), and Merker's thesis does not apply.

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Supracortical consciousness: Insights from temporal dynamics, processing-content, and olfaction

DOI: 10.1017/S0140525X07001070

Ezequiel Morsella and John A. Bargh

Department of Psychology, Yale University, New Haven, CT 06520.
ezequiel.morsella@yale.edu **john.bargh@yale.edu**
http://morsella.socialpsychology.org/

Abstract: To further illuminate the nature of conscious states, it may be progressive to integrate Merker's important contribution with what is known regarding (a) the temporal relation between conscious states and activation of the mesodiencephalic system; (b) the nature of the information (e.g., perceptual vs. premotor) involved in conscious integration; and (c) the neural correlates of olfactory consciousness.

Evidence from diverse sources has led to the consensus that conscious states integrate neural activities and information-processing structures that would otherwise be independent (Baars 2002; see review by Morsella 2005), but no such agreement has been reached regarding which neuroanatomical regions underlie this special form of integration. By reexamining long-overlooked neurological findings, Merker elegantly isolates subcortical regions that may give rise to these elusive states. With this important contribution in mind, it may be progressive to evaluate whether the temporal dynamics of these subcortical (albeit "supracortical") events are consistent with what has been documented regarding the substantial delay between afference from exteroceptors and its consciously experienced effects (see review by Libet 2005). Does activation from a supraliminal stimulus influence the mesodiencephalic system at the same time that an associated change in consciousness is predicted to occur (e.g., several hundred milliseconds following stimulus presentation; Libet 1986)? Given how much is known regarding the processing speed of the hardware at hand (e.g., neurons and synapses) and about the timings of different *stages-of-processing* as gleaned from psychophysiological recordings, answering this question may be a feasible way to obtain additional corroboratory evidence for Merker's framework. Moreover, such evidence may be in agreement with the claim that the contents of conscious states reflect the final product of a relatively timely process in which multiple, consciously impenetrable interpretations or "drafts" of sensory afference and other forms of information are entertained and evaluated (Dennett 1991).

In addition, it may be informative to evaluate whether the nature (e.g., perceptual, semantic, premotor, or motor) of the kinds of processes occurring in these integrative, supracortical regions is consistent with the view that conscious states are necessary to integrate only certain kinds of information. It is clear that many kinds of information can be integrated without these states. For example, consciously impenetrable interactions are exemplified in countless intersensory phenomena, including McGurk (McGurk & MacDonald 1976) and ventriloquism effects (Vroomen & de Gelder 2003). Indeed, it has been recently proposed that neocortical operations are essentially multisensory in nature (Ghazanfar & Schroeder 2006). That such neocortical interactions can be unconscious is consistent with Merker's proposal that cortical processes are not the seat of conscious states.

In line with Merker's "premotor" characterization of these supracortical processes and with his characterization of the "final common path," Supramodular Interaction Theory (SIT; Morsella 2005) proposes that conscious states are necessary to integrate specific, multimodal systems that are unique in that they may conflict with skeletal muscle plans, as described by the *principle of parallel responses into skeletal muscle* (PRISM). In harmony with Merker's account, these systems are defined by their concerns (e.g., bodily needs) and skeletomotor goals rather than by their sensory afference, the latter being the traditional way in which mental faculties have been characterized (Ghazanfar & Schroeder 2006). SIT illuminates why conscious states are required to integrate some processes (e.g., "pain-for-gain" scenarios as when carrying a hot plate of food or holding one's breath) but not others (e.g., intersensory interactions, peristalsis, and the pupillary reflex), and explains why skeletal muscles have been regarded as "voluntary muscles." Skeletal muscles are at times "consciously controlled" because they are directed by multiple systems that require conscious states in order to interact and collectively influence action. Accordingly, regarding processes such as digestion, one is conscious of only those phases of the processes that require coordination with skeletal muscle plans (e.g., chewing or micturating) and none of those that do not (e.g., peristalsis). Together, these proposals are consistent with the view that the properties of conscious states are intimately related to action production (Barsalou 2003; Glenberg 1997; Hommel et al. 2001; Sperry 1952), a view that challenges traditional accounts that divorce input from output processes (cf. Eimer et al. 1995).

Also consistent with Merker's account is the extensive research on "split-brain" patients and on binocular rivalry (cf. O'Shea & Corballis 2005), which strongly suggest that the minimal anatomy for a conscious brain does not require the cerebral hemispheres, nor the commissures (or transmission processes) connecting them. Moreover, although extirpation of the amygdalae and hippocampi lead to anomalies including severe deficits in affective memory (LeDoux 1996) and episodic memory (Milner 1966), respectively, it seems that an identifiable and reportable form of consciousness persists without either of these structures. It seems as well that such a minimal, conscious brain does not require interactions between the afferent impulses from the sensory organs and the initial "relay" at the thalamus, for one experiences aspects of olfaction consciously even though the signals from the olfactory sensory system bypass the thalamus and directly target regions of the ipsilateral cortex (Shepherd & Greer 1998). Of course, this does not imply that a conscious brain experiencing only olfaction does not require a thalamus. Consistent with Merker's account, in subsequent, postcortical stages of processing, the thalamus does receive inputs from cortical regions that are involved in olfactory processing (Haberly 1998).

Hence, because of its neuroanatomical accessibility and its relatively simplistic and phylogenetically primitive arrangement (Shepherd & Greer 1998), the olfactory system may prove to be a fruitful system in which to further isolate the neural processes giving rise to conscious states within the mesodiencephalic regions already identified by Merker. According to Buck (2000, p. 633), conscious aspects of odor discrimination depend primarily upon the activities of the frontal and orbitofrontal cortices, a proposal which, at least at first glance, seems inconsistent with Merker's primarily "subcortical" account of the neural correlates of conscious states. Additional research on olfactory consciousness and the olfactory components of mesodiencephalic regions may reconcile both views and thus further our understanding regarding the general nature of the physical substrates of conscious states.

ACKNOWLEDGMENT

Supported by the National Institutes of Health (R01-MH60767).

Subcortical regions and the self

DOI: 10.1017/S0140525X07001082

Georg Northoff

Laboratory of Neuroimaging and Neurophilosophy, Department of Psychiatry, Otto-von-Guericke University of Magdeburg, 39120 Magdeburg, Germany.
georg.northoff@medizin.uni-magdeburg.de
http://www.med.uni-magdeburg.de/fme/znh/kpsy/northoff/

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Abstract: Merker argues that subcortical regions are sufficient for the constitution of consciousness as "immediate, unreflective experience" as distinguished from self-consciousness. My point here is that Merker neglects the differentiation between pre-reflective self-awareness and reflective self-consciousness. Pre-reflective self-awareness allows us to immediately and unreflectively experience our self, which functionally may be mediated by what I call self-related processing in subcortical regions.

Merker argues in his article that subcortical regions are sufficient to constitute consciousness, which he defines as the ability to experience. He calls this ability "immediate, unreflective experience" (sect. 1, para. 5). This must be distinguished from states where one is aware that one is experiencing something, which he calls "additional awareness," "reflective consciousness," "reflective awareness," or "self-consciousness." He considers the cortex to be necessary only for reflective consciousness but not for consciousness as "immediate, unreflective experience." The focus is thus on subcortical regions like the substantia nigra (SN), ventral tegmental area (VTA), superior colliculi (SC), raphe nuclei (RN), hypothalamus (Hy), midbrain reticular formation (MRF), and the periaquaeductal grey (PAG). The aim of my comment is to complement Wickers' notion of consciousness as being "immediate, unreflective experience" by what I, in orientation on phenomenology (Husserl 1991; Zahavi 2005), call "pre-reflective self-awareness."

Recent imaging studies have focused on the self and observed predominantly cortical midline regions to be associated with high degrees of self-relatedness (see Northoff & Bermpohl 2004; Northoff et al. 2006). Though surprisingly little has been reported of subcortical regions (probably in part because of methodological reasons), some studies have observed their involvement in self-relatedness. Phan et al. (2004), for example, observed the association of the ventral striatum/N.accumbens (VS/NACC) with self-relatedness of emotional pictures. Similar observations with additional recruitment of the tectum, the PAG, the dorsal medial thalamus, and the colliculi have been made by Schneider et al. (submitted), though these researchers, unlike others, did not include an explicit cognitive component (e.g., decision about self-relatedness) in the activation paradigm itself. The involvement of these subcortical regions – especially the PAG and the tectum, including the SC – in processing self-relatedness has also been postulated by Panksepp (1998a; 1998b; 2003; 2005a). Based on their connectivity pattern in receiving both multiple sensory and motor afferences/efferences, these regions may be crucial in "relating" sensory and motor stimuli to the organism itself. The process of "relating" presupposes what I call self-related processing (Northoff & Bermpohl 2004; Northoff et al. 2006). Self-related processing concerns stimuli that are "experienced" as "strongly related" to the organism in its respective environmental context. "Experience" refers to the subjective aspect of experience, which is described as the "phenomenal aspect" (Block 1996; Chalmers 1996) and must be considered prereflective as distinguished from reflection, for example, cognitive aspects – this mirrors what Merker calls "immediate, unreflective experience." The term "strongly related" points out the process of associating and linking intero- and exteroceptive stimuli with a particular organism or person. The more the respective stimulus is associated with the person's sense of belongingness, the more strongly it can be related to the self. Ultimately, the self-stimulus relation results in the "immediate, unreflective experience" of what has been called "mineness" or an "addition of the 'for me'" (Lambie & Marcel 2002). What I immediately and unreflectively experience is therefore not only the stimulus itself, consciousness, but also, at the same time, myself as it is related to the stimulus – this has been called pre-reflective self-awareness. Accordingly, if subcortical regions are supposed to mediate consciousness, they may also mediate the co-occurring pre-reflective self-awareness that may explain the aforementioned involvement of these regions in imaging studies of self-relatedness.

What exactly happens in self-related processing? How can we characterize the term "process"? Instead of comparing stimuli with an absolute measure of self-relatedness, as reflected in a fixed and predefined self, stimuli are compared and matched with each other in terms of their fit and accordance. Certain interoceptive stimuli fit and match well with particular exteroceptive stimuli, whereas they do not fit well with others. For example, a highly aroused stress system causing a person excitement does not match with a rather calm and relaxing environment – the person will consequently have some difficulties in relating to this environment, which will therefore be designated as rather poorly self-related. If, in contrast, the person wants to relax and calm down, such an environment will be designated as highly self-related. Accordingly, self-related processing describes the matching and comparison between intero- and exteroceptive stimuli. This corresponds nicely to Merkers' description of the interaction between action (body), target (world), and needs (motivation), which he links with subcortical regions and which are, according to him, matched with each other. He assumes a sensorimotor-based ego-center to be the result of this matching process and distinguishes it from what he calls self-consciousness. Here I want to differentiate his terminology. What Merker describes as a sensorimotor based "ego-center" corresponds to what I and phenomenologists call pre-reflective self-awareness, an immediate and unreflective experience of the bodily based organism or person within the world. Whereas what Merker describes as self-consciousness may be more correctly termed "reflective self-consciousness."

Finally, Merker illustrates his hypothesis with the example of people without cortex, so-called hydrancephaly. His impressive description of these patients illustrates another aspect of self-relatedness, as characterized in a pre-reflective way. These patients are well able to react to salient stimuli in their environment, especially to those they are particularly familiar with, such as their parents. Self-relatedness may thus be considered a special instance of salience in general, for example, social salience. By matching intero- and exteroceptive stimuli with regard to their belongingness to the person, self-related processing allows the person to react to and navigate within a given environment and distinguish its various components according to their social salience. The case of hydranecephalic patients thus illustrates that self-related processing may be considered nothing but social salience, and that it can be well preserved even if one is not aware of it as such. Accordingly, self-relatedness, allowing for social salience and navigation within the environment, must be considered more basic and fundamental than the awareness of one's ability to experience oneself and to navigate within one's environment. This means in neural terms that subcortical regions are essential for consciousness and pre-reflective self-awareness because otherwise no self-related processing would be possible. Although cortical regions allowing for our ability to become aware of consciousness and pre-reflective self-awareness may be considered an additional function that allows me to write this comment about the self, this, however, is not absolutely necessary for my ability to constitute self-relatedness as social salience.

Emotional feelings originate below the neocortex: Toward a neurobiology of the soul

DOI: 10.1017/S0140525X07001094

Jaak Panksepp

Department of Veterinary Comparative Anatomy, Physiology, and Pharmacology, Washington State University, College of Veterinary Medicine, Pullman, WA 99164-6520.

jpanksepp@vetmed.wsu.edu

http://www.vetmed.wsu.edu/depts-vcapp/Panksepp-endowed.asp

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Abstract: Disregard of primary-process consciousness is endemic in mind science. Most neuroscientists subscribe to ruthless reductionism whereby mental qualities are discarded in preference for neuronal functions. Such ideas often lead to envisioning other animals, and all too often other humans, as unfeeling zombies. Merker correctly highlights how the roots of consciousness exist in ancient neural territories we share, remarkably homologously, with all the other vertebrates.

A cortical view of consciousness has become so prevalent that several generations of research related to the subcortical foundations of consciousness almost disappeared from reasoned discourse during the last few decades. Merker provides a long-overdue corrective. He envisions how brainstem functions are foundational for phenomenal experience as being more than simply arousal.

Consciousness is not critically related to being smart; it is not just clever information-processing. Consciousness is the experience of body and world, without necessarily understanding what one is experiencing. Primary phenomenal states have two distinct but highly interactive branches: (1) the ability to perceive and orient in the world, and (2) the ability to feel the biological values of existence. Merker has focused on the former. I will focus on the latter – the primary *affects*, from bodily hungers to emotional delights. If we get the foundational issues right, then the secondary and tertiary layers of consciousness – the ability to have thoughts about the world and thoughts about thoughts – should become easier hard problems.

Merker highlights subcortical regions as affecting primary process perceptual consciousness. Let me try to illuminate raw affective experience. Is either of these more fundamental? In mind evolution, were the perceptual or the motivational-emotional components more essential for the emergence of experiential capacities within brains? I would choose core motivational and emotional brain processes that symbolize bodily values – the diverse rewards and punishments that guide behavioral choices allowing organisms to seek comfort zones that promote survival and avoid discomfort zones that hinder survival. I suspect the more ancient, medially concentrated interoceptive motivational-emotional urges of the brainstem were foundational for the more lateral zones that harvest external information for guidance of behavior. Primary consciousness in Shewmon et al.'s (1999) neurologically impaired children was most dramatically evident in their affective presence.

Within the meso-diencephalic continuum, damage to the medial components, such as the periaqueductal gray and surrounding reticular zones, impairs consciousness more than comparable damage to surrounding tissues that process exteroceptive inputs (Panksepp 1998a; 1998b). This makes evolutionary sense if consciousness was premised on fundamental survival issues, related quite directly to organismic integrity. The most vital (least expendable) parts of the body are the viscera, neurosymbolically concentrated in centromedial regions of the mesencephalon and in the hypothalamus. Thus, neuroscientists since Hess (1957) and MacLean (1990) onward have accepted the existence of a visceral nervous system, which detects and behaviorally elaborates bodily needs. Very medial homeostatic detectors (i.e., for hunger, thirst, etc.) regulate adjacent core emotional systems that generate many distinct instinctual-emotional "intentions in action" – to use Searle's (1983) felicitous phrase.

Had William James known about such ancient brain layers, he might never have envisioned emotional feelings emanating from peripheral autonomic commotions perturbing cognitive regions of the brain – a theory that has captivated psychology to the present. Even Damasio's (1994) related somatic-marker hypothesis – placing *emotional* feeling within somatosensory cortex – remains a weak working hypothesis. That many *sensory* feelings are elaborated in insula is now well accepted. So far, there is little evidence that *peripheral bodily indices* of emotions *precede* and *cause* emotional feelings which control decision-making (Hinson et al. 2006). Had James known of the visceral-limbic brain, surely he would have considered that those networks generate emotional feelings directly (Panksepp 1998a; 2005a). Likewise, as far as we know, no Jamesian "mind-dust" permeates the universe.

If we envision three key mesencephalic-diencephalic functions as concentric circles, with (1) body need detectors situated most medially (Denton 2006), (2) emotional-instinctual systems concentrated in subsequent layers (Panksepp 1998a), and with all surrounded by (3) more externally directed somatosensory and somatomotor processes for attentive target selection and directed actions, we have a working image of primary process phenomenal consciousness. Affective consciousness, comprised heavily of the two highly interactive medial layers, may suffice for some level of experience, probably without self-awareness. Surely those emotional-instinctual layers are of foremost importance for psychiatry (Panksepp 2006). With brain maturation, additional cognitive complexities emerge upon the solid foundation of the more ancient primary processes, as Merker highlights with the compelling Sprague effect. Clearly, raw consciousness survives damage to neocortical sensory and motor homunculi.

All mind scientists should remember: Primary consciousness arises from the somato-visceral operating systems of the upper brainstem (Watt & Pincus 2004). There is something deeply personal about this kind of neural activity. This is where our bodily needs are felt (Denton 2006). These brain-mind abilities imbue experience with ownership. Perhaps subtle body representations permeate these networks of primary-process consciousness. Sensory homunculi have understandably lost appeal as necessary substrates of experience, and not just because of the illogic of infinite regress of observers. But more diffuse visceral sensory-motor integrative homunculi exist in lower regions of the brain. Just as Merker needs an "ego-center" at the core of phenomenal experience, I need a coherent core-SELF (Simple Ego-type Life Form) – a neurobiological action "soul" – as a foundation for experienced existence (Panksepp 1998a, 1998b).

There is currently little neuroscientific work on the biology of the soul, but a special issue of the *Journal of Comparative Neurology* (2005, 493:1–176), intriguingly entitled *The Anatomy of the Soul*, focused well on the subcortical depths of bodily functions, spiced with some discussion of mentality. Why do most neuroscientists remain impaled on the dilemma of how mental experience could ever emerge from physiochemical processes of the brain? This dilemma has engendered a most ruthless reductionism – where neuro-mental properties are rarely evident in discussions of what other animals do. Thus, neo-neurobehaviorism still rules: In mainstream neuroscience, other animals are generally regarded as little more than zombies. But this is an ontological presumption rather than an epistemological likelihood. By the weight of empirical evidence, all other mammals are sentient beings (Panksepp 2005a). And if we do not learn how to investigate these issues in animals, we will never have a detailed science of consciousness. It is noteworthy that the centrencephalon vision emerged first from animal research. Hopefully, Merker's powerful thesis will restore such eminent concepts to consciousness studies.

Since we still live in ruthlessly reductionistic times, let me close with a few anecdotes. When we discovered an abundant ultrasonic vocalization (USV) during rat play, we eventually conceptualized this social joy response as an ancestral form of laughter (Panksepp & Burgdorf 2003). When we first sought publication in *Nature*, a famous fear-conditioning researcher torpedoed us with this remark: "Even if their interpretation were true, they will never be able to convince their colleagues." We eventually published the ruthlessly rejected work elsewhere (Panksepp & Burgdorf 1999).

After we discovered that even complex behaviors such as play survive radical neo-decortication (Panksepp et al. 1994), I stumbled on something quite special in an undergraduate neuroscience lab: Sixteen students were each given two *adult* animals, one of which was neurologically intact, the other neo-decorticated at three days of age. After two hours of free

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

observation, the students had to decide which was which. Twelve of the decorticates were identified as normals – a statistically significant mistake! Why? Because decortication had released primary process emotionality! ... a phenomenon known since the late 19th century. Decorticates are more active, more apparently engaged, sometimes enraged, with the world. Our neurologically intact rats were more inhibited and timid (worries on their mind?).

I trust that Merker's astute analysis will not fall on deaf ears among many investigators who believe that *awareness* (knowing you experience) is the *sine qua non* of consciousness. We can all agree on the facts. When practically all higher-brain regions are removed in animals (Kolb & Tees 2000; Panksepp et al. 1994) or congenitally absent in human children (Shewmon et al. 1999), core consciousness survives. Such organisms exhibit a remarkable emotional vitality of behavior, and it is our responsibility to entertain that mentality still exists in the remnants of their brains. A science that burrows its head opportunistically in the sand is a second-rate science.

If we wish to scientifically understand the nature of primary-process consciousness, we must study the subcortical terrain where incredibly robust emotional and perceptual homologies exist in all mammalian species. Without work on animal models of consciousness, little progress, aside from the harvesting of *correlates*, can be made on this topic of ultimate concern. I appreciate Merker's timely reminder about the history of our discipline, and the need for a better understanding of animate life on earth, than any form ruthless reductionism provides.

The ontology of creature consciousness: A challenge for philosophy

DOI: 10.1017/S0140525X07001100

Gualtiero Piccinini

Department of Philosophy, University of Missouri – St. Louis, St. Louis, MO 63121-4400.

piccininig@umsl.edu **www.umsl.edu/~piccininig/**

Abstract: I appeal to Merker's theory to motivate a hypothesis about the ontology of consciousness: Creature consciousness is (at least partially) constitutive of phenomenal consciousness. Rather than elaborating theories of phenomenal consciousness couched solely in terms of state consciousness, as philosophers are fond of doing, a correct approach to phenomenal consciousness should begin with an account of creature consciousness.

A traditional question about consciousness is whether preverbal children have phenomenal experiences, and if they do, what convinces us that they do. In this context, congenitally decorticate children are not even considered worth discussing. Yet Merker argues that (some) children with hydranencephaly have phenomenal experiences. He backs up his claim with an elaborate theory supported by a wide range of evidence. To make sense of his theory, we might need to think about the ontology of consciousness in a new way.

When philosophers attempt to spell out what consciousness is, they typically formulate the problem in terms of so-called *state consciousness*: What does it take for a mental state to be an experience? Their most worked-out answers employ two kinds of ingredients: functional and representational. Their least worked-out answers appeal to some condition to be discovered empirically by scientists. For instance, pain might be C-fiber firing, or whatever scientists tell us. Well, Merker is a scientist, and he is telling us something.

Merker tells us that "primary consciousness" has the function of integrating sensory information and motivations to select targets and actions. He adds that primary consciousness is constituted by the structure of the "analog reality simulator" that fulfills this function. This may sound like a hybrid functional-representational theory. But Merker's theory does not say what it takes *for a mental state* to be conscious. It is not even formulated in terms of mental states. Furthermore, Merker attributes consciousness to some congenitally decerebrate children. How plausible is it that such children have experiences as we do? If we keep framing the question of consciousness in traditional terms – that is, in terms of what it takes for mental states to be phenomenally conscious – we seem to face a dilemma: Either decorticate children have the same kind of conscious states that we have, and hence have phenomenal consciousness, or they don't, and hence have no phenomenal consciousness. Either way, Merker has not told us what it takes to have such states. We can dismiss his theory as misguided and pursue our ontological inquiry as before.

Alternatively, we can take Merker's theory seriously and see where it leads us. Merker says his subject matter is "the state or condition presupposed by any experience whatsoever" (sect. 1, para. 2), or the "'medium' of any and all possible experience" (sect. 1, para. 3). He then gives us a detailed account of such a medium, couched in terms of neural systems, their functions, and their interrelations.

Insofar as philosophers talk about anything that sounds like this, it is what they sometimes call *creature consciousness*. For present purposes and to a first approximation, creature consciousness is whatever differentiates ordinary people who are either awake or in REM sleep from ordinary people who are in non-REM sleep, in a coma, and so forth. This seems to be what Merker is theorizing about.

When it comes to understanding phenomenal consciousness, many philosophers would maintain that creature consciousness is mostly irrelevant to the ontology of phenomenal consciousness. According to the philosophical mainstream, the ontological key to phenomenal consciousness resides in state consciousness.

Merker, however, says his subject matter is consciousness in its most "basic" sense. Perhaps he is onto something. Perhaps creature consciousness is at least partially constitutive of phenomenal consciousness. What would this mean? Most people agree that creature consciousness is a necessary condition for state consciousness. Perhaps there is more to creature consciousness than that.

From the point of view of neuroscience, creature consciousness is a global state of (part of) the brain – the difference between ordinary people's brain when they are awake or in REM sleep and their brain when they are in non-REM sleep, in a coma, and so forth. My suggestion is that creature consciousness thus understood contains at least part of the ontological basis of phenomenal consciousness. In other words, a (more or less large) part of what makes a system have experiences is that it is creature-conscious.

Under this view, state consciousness may be understood as follows: A state is state-conscious if and only if it is the state of (a spatio-temporal part of) a creature-conscious brain, or better, an appropriate kind of state of (a spatio-temporal part of) a creature-conscious brain. There remain, of course, two important questions: First, what is the difference between those states of creature-conscious beings that are phenomenally conscious and those that are not? Second, what else is needed (if anything), besides creature consciousness, for full-blown phenomenal consciousness? An adequate theory of consciousness would have to answer these questions.

What kind of global brain state corresponds to creature-consciousness? Is it physical, functional, representational, or a combination of these? According to Merker, creature consciousness is the product of an analog reality simulator that integrates sensations and motivations to select targets and actions. Perhaps his view could be glossed as follows: When the simulator is operating, the system is creature-conscious; when the simulator is idle (for whatever reason: rest, breakdown, etc.), the

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

system is creature-unconscious. Integrating sensory information and motivations as well as selecting targets and actions appear to be broadly functional and representational notions. So Merker appears to be offering a functional/representational account of creature consciousness.

There is at least one other option. Perhaps creature consciousness requires some special physical properties, analogously to the way water's power to dissolve certain substances and not others requires a certain molecular composition and molecular structure at a certain temperature (cf. Shapiro 2004). I cannot elaborate further. Differentiating clearly between physical, functional, and representational accounts of creature consciousness would require an adequate account of the distinction between the physical, the functional, and the representational, and there is no room for that here.

The present suggestion has epistemological consequences. If creature consciousness were at least partially constitutive of phenomenal consciousness, it would be a mistake to develop theories couched solely in terms of state consciousness, without saying anything about creature consciousness – as philosophers are fond of doing. Rather, a correct approach to phenomenal consciousness should begin with an account of creature consciousness.

Before concluding, it may be helpful to distinguish several different claims: (1) the brainstem is necessary to sustain and regulate creature consciousness (uncontroversial), (2) the brainstem can sustain creature consciousness by itself (Merker's theory), (3) the brainstem can be the locus of conscious experience (Merker's theory), and (4) creature consciousness is (at least part of) the ontological basis of conscious experience.

Thesis (3) is stronger than (2), and Merker does little to support (3) as opposed to (2). (Do children with hydranencephaly go into anything resembling REM sleep? Evidence that they do would support [3].) Perhaps he intends to make a further claim: (5) creature consciousness is sufficient for phenomenal consciousness. Thesis (5) is even stronger than (4). However, in light of unconscious cognition, including phenomena such as blindsight, (5) is hard to swallow without at least some qualification.

But we don't need to accept all of Merker's claims in order to consider (4). In fact, claim (4) can be motivated on the grounds of (2) or even (1) alone, and (1) is uncontroversial. If phenomenal consciousness can occur without a cortex, as Merker believes, then the challenge posed by (4) becomes more forceful and more difficult to avoid. But, regardless of the extent to which we agree to Merker's theory, we should consider the possibility that (4) is correct.

ACKNOWLEDGMENTS

Thanks to Brit Brogaard, Bob Gordon, Pete Mandik, Brendan Ritchie, and Anna-Mari Rusanen for discussion and comments.

Who dominates who in the dark basements of the brain?

DOI: 10.1017/S0140525X07001112

Tony J. Prescott and Mark D. Humphries

Department of Psychology, University of Sheffield, Sheffield, S10 2TN, United Kingdom.

t.j.prescott@sheffield.ac.uk http://www.abrg.group.shef.ac.uk/tony/
m.d.humphries@sheffield.ac.uk http://www.abrg.group.shef.ac.uk/mark/

Abstract: Subcortical substrates for behavioural integration include the fore/midbrain nuclei of the basal ganglia and the hindbrain medial reticular formation. The midbrain superior colliculus requires basal ganglia disinhibition in order to generate orienting movements. The colliculus should therefore be seen as one of many competitors vying for control of the body's effector systems with the basal ganglia acting as the key arbiter.

Understanding the brain's functional architecture is certainly key to unlocking the mystery of the coherence of behaviour, and even, perhaps, consciousness. In this regard, Merker usefully draws our attention to subcortical systems as critical loci for behavioural integration that may instantiate some form of supra-cortical control. As we have previously argued (Prescott et al. 1999), combining Penfield's notion of a centrencephalic dimension to brain organization with a view of the brain as a layered control system provides a powerful set of explanatory concepts for understanding how the vertebrate brain architecture has adapted, with little change to its basic "groundplan," to many different body types and ecological niches. The particular set of brainstem substrates that Merker has chosen to emphasize seems, however, somewhat curious. The roles of the colliculus in orienting, the periaquaductal grey in behavioral patterning, and the hypothalamus in motivation are not controversial, but the promotion of the colliculus to the "functional apex" of processing for target selection is surprising, as is the suggestion of the zona incerta (ZI) as a key locus for action selection. In our view, other centres, either side (i.e., both more rostral and more caudal) of Merker's "selection triangle," may be more important in subserving these important aspects of behavioural integration.

One such group of structures are the basal ganglia (BG). This collection of fore- and mid-brain nuclei, identified by Thompson (1993) as a major component of the centrencephalic core, is located in such a way that its principal input structure (striatum) is rostral, and its output structure, substantia nigra (SNr), caudal to Merker's "synencephalic bottleneck." The BG are therefore ideally placed to provide the required funnel from distributed cortical processing to sequential brainstem operation. Merker discusses the functional role of the BG, primarily in relation to this "data reduction" context, as providing action-related information to the colliculus. However, the BG appear to be doing something more significant than simply providing the colliculus with one of its several sources of afferent input. Specifically, the tonic inhibition provided by the SNr maintains a veto over the capacity of the colliculus to generate orienting movements (Hikosaka et al. 2000). In the case of a visual stimulus, for example, this veto is only removed when there is sufficient excitatory input onto the oculomotor region of the striatum to cause inhibition of SNr and, thence, disinhibition of the collicular motor layer. The colliculus itself provides afferent input (via thalamus) to relevant striatal neurons that, together with convergent signals from cortex, the limbic system, and elsewhere, determine the significance of the stimulus (McHaffie et al. 2005). It is therefore the BG, not the colliculus, that sees the full gamut of pertinent, contextual information and is thus the dominant partner. Without BG gating, the colliculus would initiate orienting to any target that generated a strong, spatially localized phasic stimulus. The BG add intelligence to this reactive process by preventing orienting to high-amplitude but uninteresting stimuli, and enabling it to weaker, but potentially more significant, triggers. A broad range of empirical studies, theoretical proposals, and computational models (for reviews see Gurney et al. 2004; Redgrave et al. 1999) support the proposal that the BG operate as an action selection mechanism, not just for collicular control of orienting, but for competing sensorimotor systems throughout the brain. From this perspective, the colliculus is just one of many competitors vying for control of the body's effector mechanisms, with the BG as the key arbiter.

A remarkable feature of the BG is the homogeneity of their intrinsic circuitry. This observation adds weight to the hypothesis that these nuclei implement a consistent function despite

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

the functional diversity of brain areas to which they interface. In contrast, the ZI, highlighted by Merker as a possible action selection locus, is a very heterogeneous structure (Mitrofanis 2005). Furthermore, evidence from functional studies suggests other possible modulating roles: for instance, Trageser et al. (2006) reported ZI's involvement in gating ascending sensory inputs according to the animal's current state of arousal.

Although the BG instantiate a dominant integrative centre in the intact adult brain, studies of infant and decerebrate rats suggest the presence of an alternative locus for action integration further down the neuraxis. A possible candidate, first suggested by the Scheibels (1967), is the medial core of the reticular formation (mRF). This hindbrain structure receives input from many cortical and subcortical brain systems and directs its output to movement generators in the brainstem and spinal cord. We recently sought to promote interest in the mRF by elucidating its anatomy (Humphries et al. 2006), and by developing new simulation and robotic models of this structure viewed as an action selection mechanism (Humphries et al., in press). The mRF is organized as a set of linearly arranged cell clusters, likened by the Scheibels to a "stack of poker chips." In Humphries et al. (in press) we proposed, and demonstrated in simulation, that activity in individual clusters may represent *sub-actions* – component parts of a complete behavior. Effective control by the mRF would therefore involve simultaneous activation of clusters representing compatible subactions and inhibition of clusters representing incompatible ones. The mRF is a major target of BG output (via the pedunculopontine nucleus) and, in the intact adult brain, both systems are likely to cooperate in determining what behaviour is expressed at a given time. The relationship between the two systems may combine aspects of layered and hierarchical decomposition of control. Layered, because developmental and lesion studies suggest that the mRF can operate, to some degree, without modulation from higher brain structures (including BG). Hierarchical, because patterns of mRF coordinated behavior could be selected *in toto* by BG focal disinhibition.

For Wilson (1925), the BG, lying towards the base of the brain, had "the characteristic of all basements, i.e. darkness." Although many windows have been opened onto BG function since Wilson's era, other subcortical nuclei still reside in subterranean obscurity. Despite the gaps in our knowledge, Merker is right to try to discern some structure amidst the gloom. With regard to his specific hypotheses, however, there is no compelling reason for viewing the ZI as the central arbiter, or the colliculus as the target selector. In the dark basements of the brain the basal ganglia dominate both.

Should the superficial superior colliculus be part of Merker's mesodiencephalic system?

DOI: 10.1017/S0140525X07001124

John Schlag

Department of Neurobiology, School of Medicine, UCLA, Los Angeles, CA 90095-1763.

jschlag@ucla.edu

Abstract: The superficial superior colliculus appears to be a primitive visual analyzer whose function has been taken over by the visual cortex, most completely in man. The phenomenon of blindsight shows that, although intact, the superior colliculus cannot by itself provide conscious perception in human patients. Is it possible that, in anencephalic children, it recovers the role it had in lower mammals?

Nowadays, we tend to believe that all brain functions are localized. The reason is that modern techniques – from unit recordings in behaving animals to fMRI in humans – are geared to finding functions localized. It can hardly be otherwise, because data obtained by these techniques are publishable only if they lead to the discovery that the particular behavior or function under study can be attributed to a given structure or type of neurons. If the research finds no such evidence, the data will not be published. Thus is introduced an obvious bias in our views, and it is unfortunate because some functions may depend more on circuits of interactions between different structures than on the activation of neurons in any one of these structures particularly. The target article by Björn Merker adopts another approach. It is a refreshing effort of integration. The problem of consciousness is among the most difficult, because consciousness is so hard to define, difficult to test, and it seems to depend on the integrity of a number of functions (albeit none of them absolutely essential in all situations), such as memory, perception, attention, emotional concern, language, and other motor behaviors – even laughing. Indeed, laughing happens to be one of the criteria that Merker uses in evaluating the conscious state of anencephalic children.

I think that Merker is right in pointing out that consciousness is neither obviously nor necessarily a cortical function. His anecdotal observations of anencephalic children are impressive and important, both from scientific and ethical viewpoints. Merker stresses the role of a mesodiencephalic group of structures and I agree on this idea, but I am a little surprised to see included in this group the superior colliculus or, at least, its superficial layers.

The most superficial layers of the superior colliculus are essentially visual. Their organization is certainly more primitive than that of primary visual cortex, but still, it is topographic. It is probably relevant to consider the phenomenon of blindsight (Weiskrantz et al. 1974) in discussing the possible participation of the superior colliculus in consciousness. Patients who have a circumscribed lesion of their primary visual cortex are blind in the corresponding region of their contralateral visual field. They say that they don't perceive a visual stimulus presented in that region. Yet, when forced to do so, they can report the presence or absence of such a stimulus with surprising accuracy. Even features like size or orientation often are "guessed" correctly. The phenomenon of blindsight suggests a couple of remarks.

First, because conscious perception is lost in blindsight but the superior colliculus is intact, it is difficult to argue that the latter plays a major role in consciousness in an adult human brain. Maybe, in an anencephalic child, the superior colliculus has recovered the function of visual analyzer that has been transferred to the cerebral cortex during the course of evolution.

Second, as visual discrimination is spared – at least partly – but conscious perception is lost in human blindsight, it also seems difficult to take the persistence of visual discrimination after brain lesion in primates as evidence relevant to consciousness. Visual discrimination can exist without consciousness.

The superior colliculus has been one of the most thoroughly investigated structures in rodents (hamsters and rats), in cat, and in monkey, in whom it plays a significant role in vision. In these species, the visual physiology of the upper layers of SC has been as abundantly studied as that of visual area V1. But, remarkably, we have much less information about the significance (if any) of the superior colliculus in man. There is remarkably little known pathology of the superior colliculus (e.g., in contrast to more ventral structures such as the interstitial nucleus of Cajal, the medial longitudinal fasciculus, the red nucleus, and reticular formation). It is quite conceivable, in fact, that the human superficial superior colliculus is no more than a remnant of an ancient visual analyzer. In contrast, the deeper superior colliculus is structurally more like the adjacent mesencephalic reticular

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

formation and could, indeed, be a part of the system described by Merker.

The functional utility of consciousness depends on content as well as on state

DOI: 10.1017/S0140525X07001136

Anil K. Seth

Department of Informatics, University of Sussex, Falmer, Brighton, BN1 9QH, United Kingdom.

a.k.seth@sussex.ac.uk

http://www.informatics.sussex.ac.uk/users/anils/

Abstract: This commentary considers Merker's mesodiencephalic proposal in relation to quantitative measures of neural dynamics suggested to be relevant to consciousness. I suggest that even if critical neural mechanisms turn out to be subcortical, the functional utility of consciousness will depend on the rich conscious contents generated by continuous interaction of such mechanisms with a thalamocortical envelope.

Merker's target article provides a lucid and compelling alternative to currently dominant (thalamo-)corticocentric proposals regarding the loci of neural mechanisms underlying consciousness. Taking a quantitative perspective, this commentary challenges Merker's claim that the functional utility of consciousness is independent of the level of sophistication at which conscious contents are integrated. I also comment on the proposed function of consciousness in the coordination of motivation, action, and target selection, and finally, I suggest some implications for nonhuman consciousness.

An important step in the evolution of scientific theory is the development of useful quantitative measures that connect different levels of description. The scientific study of consciousness requires such measures in order to generate explanatory links between features of neural activity and features of phenomenal experience. Several recent studies have discussed various measures of the "dynamical complexity" of neural activity, including "neural complexity" (Edelman & Tononi 2000; Tononi & Edelman 1998), "information integration" (Tononi 2004), and "causal density" (Seth 2005; Seth et al. 2006). These measures share the idea that the dynamical complexity of a neural system reflects the extent to which the activity of its components is both *differentiated* (i.e., small subsets of a system are relatively independent of each other) and at the same time *integrated* (i.e., large subsets tend to behave coherently).

Critically for theories of consciousness, the balance between differentiation and integration is also a fundamental aspect of phenomenal experience: Each conscious scene is one among a vast repertoire of possible conscious scenes (differentiation) and yet is experienced as a unified whole (integration) (Tononi & Edelman 1998). Therefore, a well-specified measure of dynamical complexity can provide an explanatory link between neural activity and phenomenal experience. Importantly, cortical networks appear particularly well suited to generating neural dynamics of high complexity (Sporns et al. 2000).

The detailed description of mesodiencephalic mechanisms provided by Merker raises the interesting possibility that mesodiencephalic and corticocentric models could be compared on their propensity to generate complex neural dynamics. Although such modeling work remains to be done, it seems plausible that a model mesodiencephalon by itself would *not* support neural activity of high dynamical complexity, at least when compared to a model thalamocortical system. Why? Previous computational models of closely associated mechanisms that are also involved in sensorimotor selection, such as the basal ganglia and the medial reticular formation, reveal dynamical properties appropriate for segregation of multiple competing sensorimotor streams (Humphries et al., in press; Prescott et al. 1999). Such dynamical segregation seems inconsistent with the integration required for high values of complexity. Moreover, the small size of mesodiencephalic systems as compared to thalamocortical systems, in terms of numbers of neuronal elements, suggests that the latter should support dynamics with greater differentiation.

Having dynamics of high complexity is important not only in accounting for fundamental aspects of phenomenology, but also for supplying functional utility. According to the "dynamic core hypothesis" of Edelman and Tononi (2000) and its recent extensions (Edelman 2003; Seth et al. 2006), the functional utility of a complex neural/phenomenal state is that it provides a highly informative *discrimination*. By being differentiated, any given conscious state is distinct from an enormous repertoire of other states, each reflecting different combinations of internal and external signals. By being integrated, each conscious state can appear as distinct *to the system itself*, and is therefore useful *for* the system in guiding action.

This position differs from Merker's claim that the functional utility of consciousness "will turn out to be independent of the level of sophistication at which the contents it integrates are defined" (sect. 1, para. 6). From the point of view of discrimination, functional utility will correlate closely with the sophistication of conscious contents. A richly elaborated conscious scene will provide a more informative and hence a more useful discrimination than a comparatively impoverished scene. In other words, the functional utility of consciousness should not be construed only in terms of conscious "state" (i.e., a position on a continuum ranging from coma to normal alert wakefulness), independent of the degree of elaboration of conscious "content" (i.e., the richly differentiated components of each conscious experience). As Merker makes clear, subcortical mechanisms are proposed as a locus for the generation of conscious state, whereas conscious contents remain dependent on cortex. Thus, even if critical neural substrates turn out to be subcortical, the functional utility of consciousness will depend on cortical systems, as well.

Merker himself argues that consciousness is useful for integrating target selection, motivational modulation, and action selection. This proposal marks a valuable departure from many previous studies, which, possibly for reasons of practical necessity and misplaced conceptual hygiene, treated these overlapping and interdependent processes as being in principle separable and independent (see Seth [in press] for further discussion of this issue). Merker's proposal can also be viewed in terms of discrimination, because each integration can be thought of as being an informative discrimination among a repertoire of motivationally modulated sensorimotor mappings. Moreover, that such integrations are suggested by Merker to take place in a conscious "analog reality space" parallels the dynamic core hypothesis in proposing that conscious qualia *are* high-order discriminations in a multidimensional signal space (Edelman 2003).

Finally, it is worth considering the important question of nonhuman consciousness. A strong case can be made that the ability of organisms to verbally report conscious contents should *not* be taken as a necessary criterion for consciousness (Seth et al. 2005). Rather, by using humans as a benchmark, a number of interlocking criteria can be identified, at both behavioral and neurophysiological levels of description. These criteria include "informativeness" as measured by dynamical complexity. Whereas in humans and other mammals the relevant dynamical complexity may depend on the interaction of a mesodiencephalic system with a thalamocortical system, in non-mammals it may depend on different anatomies, for example, a differentiated telencephalon in birds, and the optic, and vertical, and superior lobes in cephalopods (Edelman et al. 2005). In any case, by shifting the theoretical spotlight away from cortex and towards architectonic features that are conserved among a wider range of species, Merker's article lies squarely in the productive tradition of challenging human and mammalian privilege.

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Raw feeling: A model for affective consciousness

DOI: 10.1017/S0140525X07001148

Jack van Honk[a], Barak E. Morgan[b], and Dennis J. L. G. Schutter[a]

[a]*Experimental Psychology, Department of Psychology, Utrecht University, 3584CS Utrecht, The Netherlands;* [b]*Department of Human Biology, Health Sciences Faculty, University of Cape Town, 7975 Cape Town, South Africa.*

j.vanhonk@fss.uu.nl **bmorgan@cormack.uct.ac.za**
d.schutter@fss.uu.nl

Abstract: Seeking to unlock the secrets of consciousness, neuroscientists have been studying neural correlates of sensory awareness, such as meaningless randomly moving dots. But in the natural world of species' survival, "raw feelings" mediate conscious adaptive responses. Merker connects the brainstem with vigilance, orientating, and emotional consciousness. However, depending on the brain's phylogenetic level, raw feeling takes particular forms.

Philosophical debate on consciousness is ageless, but detailed neurobiological models are a recent development. One of the best among the latter is global workspace theory (GWT; Baars 1988); which subscribes to the traditional definition of consciousness as subjective awareness of momentary experience interpreted in the context of memorized past and expected future. Consciousness in the "cortico-centric" GWT is conceived of as transient synchronized thalamo-cortico-cortical neural activity.

The GWT-like framework of Crick and Koch (1998; 2003), attempts to reduce consciousness to measurable properties by explicitly leaving out emotions and feelings. But what remains in such accounts of consciousness? Conversely, a growing body of theory maintains that the study of consciousness and emotion will yield new insights (Damasio 1999; Greenfield 2000). The theoretical analysis of Merker, supported by his notable findings in hydranencephalic children, adds important impetus to this movement.

Consciousness and emotion. Fundamental insights have been gained by studying "purely cognitive" processing, but virtually all conscious experience carries an affective tone (Ashton 2002). This affective tone, designated as "raw feeling" (Panksepp & Panksepp 2000) influences information processing faculties such as attention, memory, and decision-making, which have been associated with consciousness in both traditional and contemporary theories (Baars 1988; Damasio 1999).

Panksepp and Panksepp (2000) broke the boundaries of traditional theories of consciousness by proposing a double-layered model wherein a secondary cortico-centered form supervenes on a subcortico-centered primary form of consciousness. According to Panksepp and Panksepp (2000), brain evolution shows that the secondary cognitive forms of consciousness emerged from the primary affective forms. Moreover, they argue that our "raw emotional experiences" are created subcortically and constitute the primordial neural ground upon which all forms of conscious processing are built. Emotions, therefore, do not merely provide for "global valence tagging" in the cognitive realm, but mediate the subject's strategic quest for adaptive homeostasis in both immediate (e.g., hunger, thirst, fear, anger) and more enduring timeframes (e.g., goal-directed behavior, dominance status, attachment/bonding) (Schutter & Van Honk 2004a; Van Honk & Schutter 2005). In the next subsection, a triple-layered model of "affective consciousness" adapted from Panksepp and Panksepp (2000) is outlined. It might serve the psychobiological investigation of embodied awareness in a manner consistent with the compelling hydranencephalic evidence amassed by Merker against the exclusively cortical model of consciousness.

A model of affective consciousness. Consciousness evolved to ensure adaptive homeostasis (Damasio 1999; Panksepp & Panksepp 2000; Schutter & Van Honk 2004b). The mechanism relies on the subject's capacity to experience raw feelings of reward and punishment, which evoke functional behavioral responses. This core feature works together with the ability to detect (on basis of motivated attention) and to evaluate (on basis of instinct/emotional memory) rewards and punishments and to make fine-tuned decisions of approach or withdrawal-related action (Ressler 2004; Schutter & Van Honk 2004b). Reminiscent of the triune brain theory of Paul MacLean (1990), we propose a theoretical framework which encompasses three detection-evaluation-decision (DED) devices that mirror phylogenesis observed in the instinctual reptilian, emotional paleomammalian, and cognitive neomammalian brain (cf. Panksepp 2005a for a related but more strongly bottom-up regulated 3-level model). These DED devices are concordantly instinctual, emotional, and cognitive in nature, but their working is also orchestrated by raw feelings that, depending on the level, come as instinctual drives, emotional biases, and cognitively guided mood states.

On the different phylogenetic levels there are structural convergence zones wherein core brain areas influence the content of affective consciousness. In the reptilian brain, DED processing occurs at an instinctual brainstem level. For example, on its most primitive level, the vagus reflexively copes with threat by way of immobilization behaviors such as passive avoidance (Porges 2001). Crucially, there is evidence showing that parasympathetically mediated immobilization behaviors are mediated by raw feelings in the form of instinctual drives (e.g., Hofer 1994). Thus, primordial DED processing at the level of the vagus nerve is instinctual, implicit, and therefore of a non-cognitive nature.

In the paleomammalian or emotional brain, the DED system copes with threat by initiating flight/fight behaviors that are modulated by neuroendocrine mechanisms at the level of the amygdala and hypothalamus (Van Honk & Schutter 2005). The involvement of the amygdala in different aspects of affective processing is especially well documented. This small medial temporal lobe structure has extensive connections with all major subcortical and cortical structures involved in motivation, emotion, and emotion regulation. Receiving information indirectly from the sensory cortices and directly from the thalamus, the amygdala participates in both implicit and explicit forms of DED processing (Davis & Whalen 2001; LeDoux 2002). Orchestrated by raw feelings in the form of emotions, the amygdala DED mechanism copes with threat by initiating flight-fight behaviors.

The neomammalian-cognitive brain possesses our higher-order cognitive faculties such as reasoning and language (Damasio 1994). Affective consciousness is not rooted here but can be accessed and modulated in a top-down fashion (Block 1995). A brain structure importantly involved in cognitive emotional DED processing is the orbitofrontal cortex (OFC) (Rolls 1999), which is highly interconnected with other cortical and subcortical brain areas. At the level of the OFC, motivated behavior is explicit, cognitively controlled, and effortful in nature. Behavior also carries social features, and the arsenal of responses to challenges employed by DED include instrumental acts wherein complex emotion-cognition interactions take place. All of these are directed by raw feelings in the form of cognitively laden mood states.

These are the core principles of our perspective on affective consciousness, a triple-layered instinctual-emotional-cognitive adaptation that follows the phylogeny and ontogeny of brain development and wherein reverberating neurodynamic affective maps are continuously created at the brain's phylogenetic levels. These affective maps constitute raw feelings on different processing levels in the brain – a triple balance supporting global adaptive homeostasis bound into a unitary experience. However, drawing upon Jackson's (1958) principle of dissolution, MacLean's (1990) notion of loosely coupled systems, and the polyvagal theory of Porges (2001), important insights can be

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

gained into consciousness by scrutinizing evolutionarily separate functions on behavioral and physiological levels. Merker's story provides some of these insights and may contribute importantly to theories on the "what and where" of consciousness.

ACKNOWLEDGMENT

This work was sponsored by an Innovational Research Grant (# 016-005-060) from the Netherlands Organization for Scientific Research.

The human superior colliculus: Neither necessary, nor sufficient for consciousness?

DOI: 10.1017/S0140525X0700115X

Susanne Watkins and Geraint Rees

Wellcome Trust Centre for Neuroimaging and Institute for Cognitive Neuroscience, University College London, London WC1 N 3AR, United Kingdom.

s.watkins@fil.ion.ucl.ac.uk **g.rees@fil.ion.ucl.ac.uk**

http://www.fil.ion.ucl.ac.uk/~grees

Abstract: Non-invasive neuroimaging in humans permits direct investigation of the potential role for mesodiencephalic structures in consciousness. Activity in the superior colliculus can be correlated with the contents of consciousness, but it can be also identified for stimuli of which the subject is unaware; and consciousness of some types of visual stimuli may not require the superior colliculus.

Merker presents a wide-ranging overview in which a central role for the mesodiencephalic system in consciousness is proposed. Specifically, it is suggested that activity in the superior colliculus (SC) is necessary for changes in conscious content to occur, and activity in mesodiencephalic structures is sufficient to support consciousness. In humans, there is increasing evidence that activity in subcortical structures, such as the SC, can indeed be correlated with the contents of consciousness. Human SC is visually responsive in a retinotopic fashion (Schneider & Kastner 2005; Sylvester et al. 2007), and Merker highlights our recent demonstration that changes in SC activity (accompanied by similar changes in activity in retinotopic early visual cortex) are correlated with altered perception in a visual illusion induced by sound (Watkins et al. 2006). Moreover, other subcortical structures anatomically adjacent and closely linked to the SC, such as the lateral geniculate nucleus, show fluctuations in activity closely correlated with changes in the contents of consciousness during binocular rivalry (Haynes et al. 2005; Wunderlich et al. 2005). But after damage to human primary visual cortex, SC activity can also be observed when moving visual stimuli are presented in a blind hemifield (Sahraie et al. 1997). Moreover, such SC activation can correlate with the emotional content of faces again presented in the blind hemifield (Morris et al. 2001). Such processing of subjectively invisible visual stimuli associated with SC activation can be associated with residual visual sensitivity (or "blindsight"; Weiskrantz 1997), which in turn may be related to different patterns of SC connectivity in patients with blindsight following hemispherectomy (Leh et al. 2006). Taken together, these data suggest that activation of the superior colliculus alone is therefore not *sufficient* for awareness, at least after damage to primary visual cortex.

The notion that activity in mesodiencephalic structures alone is insufficient to support consciousness is challenged by Merker's fascinating personal observations of the behavior of children with hydranencephaly. Despite these children apparently lacking most functioning cortical structures, a range of behaviors is reported that indicates some degree of limited responsiveness to their surroundings. However, caution is required before concluding that these individuals are conscious, and indeed, interpreting this as reflecting preserved mesodiencephalic function. Hydranencephaly describes a range of brain malformations that may vary with respect to time of onset, pathogenesis, and organization of any cortical remnants that may be present (Halsey 1987); and survival beyond six months is rare (McAbee et al. 2000). In the presently reported cases, the extent of cortical damage is unclear, so the extent to which any behaviors reflect mesodiencephalic structures alone in these individuals is not known. Moreover, responsiveness to the environment is a capacity exhibited by nearly any organism with a central nervous system, and cannot be unambiguously taken as a marker of consciousness. Verbal or manual reports are generally considered the primary criterion that can establish whether a percept is conscious (Weiskrantz 1997). Such behaviors, demonstrating intentionality, are not clearly evident in the present observations and many of the reported behaviors could be generated unconsciously or reflexively. This emphasizes both the difficulty in determining whether an individual unable or unwilling to give verbal or manual reports is conscious (Owen et al. 2006), and the consequent need to explore the possibility that non-invasive biomarkers of consciousness might be developed to permit such inference.

Three indirect lines of evidence also suggest that SC activation in humans may not be necessary, either, for changes in the contents of consciousness to occur. First, visual stimuli that stimulate only short-wave-sensitive cones (S-cones) in the retina are clearly visible (and indeed can influence attention and behavior; Sumner et al. 2006), even though the SC receives no direct projections from short-wave-sensitive cones and is therefore unlikely to be activated by such stimuli. Second, although SC damage in humans can cause lateralized visual neglect (Sprague 1996) and consequent failure to represent the contents of consciousness in one half of the space, bilateral damage does not eliminate awareness (Weddell 2004). Finally, direct intracranial stimulation of human visual cortex that bypasses geniculostriate and retinotectal pathways can result in conscious visual percepts (Lee et al. 2000), suggesting that subcortical activity may not be necessary for all types of awareness. Although all these lines of evidence are indirect, they raise the question of whether SC activity is strictly necessary for all types of conscious visual percept.

The picture that emerges, at least in humans, appears to be more complex than a simple identification of particular parts of the mesodiencephalic system with a single role as a necessary and sufficient "gatekeeper" for the contents of consciousness. Indeed, it seems unlikely that activity in any single area of the human brain will be sufficient for consciousness (Rees et al. 2002). The consistent association of changes in activity in SC (and other subcortical) structures with fluctuations in awareness thus suggests that they may play a role as part of a network of cortical and subcortical areas whose activity might represent a minimally sufficient substrate for the contents of consciousness; but further research is required.

ACKNOWLEDGMENT

This work was supported by the Wellcome Trust.

Affirmative-action for the brainstem in the neuroscience of consciousness: The zeitgeist of the brainstem as a "dumb arousal" system

DOI: 10.1017/S0140525X07001161

Douglas F. Watt

Clinic for Cognitive Disorders, Neuropsychology Department, Quincy Medical Center, Quincy, MA 02169; and Boston University School of Medicine, Boston, MA. 02118.

dfwatt@rcn.com

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Abstract: Merker offers a remarkable statement about the neural integration essential to conscious states provided by the mesodiencephalon. The model for triangular interaction between action selection, target selection, and emotion is heuristic. Unfortunately, there is little interest (relatively speaking) in neuroscience in the mesodiencephalon, and attention is currently heavily directed to the telencephalon. This suggests that there may be less real momentum than commonly assumed towards the Holy Grail of neuroscience, a scientific theory of mind, despite the major upsurge in interest.

It is a great privilege to comment on such a remarkable and brilliantly integrative essay. Although bits and pieces of this argument have been in the literature in various forms for a while, the full and extended summation of them in the target article is original, and at the same time, timely and badly needed. It is urgently needed at a time when the equation of consciousness with cortical function, if anything, is only deepening in neuroscience, particularly within cognitive neuroscience, where functional imaging study after study generates images showing (primarily, albeit not exclusively) cortical activation.

Neuroscience still fundamentally lacks its keystone, a validated theory of consciousness. I agree strongly with Merker that until we understand the complexity of the deep integrations taking place within many dozens of brainstem structures and then their interdigitation with thalamus and cortex, we will move no closer to the Holy Grail of neuroscience – that is, a neural theory of mind. That consciousness must rest in some form of neurodynamic integration seems the only certainty. That it might be marked in cortex by higher frequency oscillations putatively linking distributed cortical regions does not help us understand what the requisite and essential neurodynamics of the upper brainstem might be. Only the superior colliculus (SC) appears to follow the gamma and beta oscillatory pathways of cortex.

Merker's article starts with the central heuristic that consciousness is a way of matching needs with opportunities as part of a centralized interface for action and target selection. He describes consciousness as arising out of a "motion-stabilized body–world interface" (sect. 7), presenting potential targets for action, while motivational systems "bid" competitively into that interface to both select targets and also to select actions. I believe he is correct that consciousness must bring together target selection, action selection, and motivation to optimize integration for action in real time, with the integration highly adaptive and selected on this basis. In other words, consciousness may *emerge from* interdigitation of attention, action selection, and emotion/homeostasis. These concepts are very similar to those I independently presented in a previous publication with a colleague, and in an ASSC (Association for the Scientific Study of Consciousness) electronic seminar[1] (Watt & Pincus 2004; Watt 1998). Jaak Panksepp has also separately suggested that consciousness is dependent on the integration of sensory maps, motor maps, and homeostatic/affective information (Panksepp 1998a), and Damasio has proposed somewhat similar notions (1999). The issue here is not "who came up with the idea first," but rather that *different theorists and researchers are coming to essentially the same conclusion quite independently of one another*. Thus, despite the chaos in the neuroscience of consciousness, a broad-based confluence of ideas is forming in a still inchoate form.

To create any kind of theory of conscious state without first considering how the brain might integrate sensory processing, and motor processing with emotional/homeostatic processing seems a doomed venture. The phenomenological/behavioral priority of experiences such as hunger and pain argue that homeostasis has "ground floor" involvement in the machinery of consciousness, consistent with selection mandating that consciousness promote survival by *prioritizing* homeostasis. As the simplest and most basic paradigm for consciousness, sensory systems mapping an image of food, motor systems mapping trajectories to the food, and a homeostatic representation of metabolic shortfall must be in register with one another in order for an organism to do something as simple as eat when energy is low, in the presence of food. I suspect this integration of motor and sensory and homeostatic operators may not only be taking place between the colliculi, periaquaductal gray (PAG), and motor systems in the brainstem as outlined by Merker, but also within the "extended reticular thalamic activating system" (Newman & Baars 1993) Therefore, it might be more accurate to characterize these as "smart integration systems" rather than as "dumb arousal systems."

This notion of the reticular brainstem as a "dumb arousal system" is complementary to the assumption that "consciousness is in the cortex." The concept of a dumb arousal system suggests that the brainstem does for the forebrain essentially what a battery does for a light. This "dumb arousal" concept is a begrudging acknowledgment of the original work by Moruzzi and Magoun (1949) on the reticular activating system, but it is far less than the system-wide functional integration that Merker argues is the real contribution of the mesodiencephalon. The "dumb arousal" concept (in my judgment) may have actually set back (more than we appreciate) a truer functional understanding of the brainstem and indeed of consciousness itself. The "dumb arousal" concept also generated a naïve optimism that we could compensate for brainstem injuries that caused severe disorders of consciousness through brainstem or thalamic electrical stimulation therapies. By and large, these have been spectacularly unsuccessful. Perhaps we are missing something. Certainly such a simple concept could do little justice to the functional complexity of the brainstem, which contains 40+ nuclei, with a staggering diversity of connections, neuromodulators, and functional correlates.

A question rarely asked about this concept for the reticular brainstem as a "nonspecific arousal system" is, "what does this *really* mean?" First of all, the notion of arousal as being "nonspecific" is clearly mistaken from the standpoint of widely differential contributions from these many reticular activating system structures. Additionally, the notion of "arousal" itself has been used in several different ways: (1) any process that increases firing rates of distributed forebrain neurons; (2) affective arousal (as in states of anger); and (3) global state shifts, such as into wakefulness, dreaming, and various stages of sleep. The first meaning (increased firing rates in forebrain) is not an adequate explanation at a neurodynamic level for the achievement of arousal in behavioral/affective terms, or for arousal to wakefulness, as consciousness cannot be meaningfully explained by the simple notion of "increased firing of forebrain neurons under brainstem influence." Lastly, arousal, as in simple arousal to wakefulness, is not a remotely adequate functional correlate for the extended RAS (reticular activating system), as wakefulness is preserved in PVS (persistent vegetative state), where no consciousness is present, often in the context of extensive RAS-mesodiencephalic lesions. Hence, "arousal to a conscious state" cannot be conflated with any kind of simple wakefulness, and requires other integrative functional "envelopes" (core/constitutive functions of attention, intention, and emotion). Therefore, if "arousal" simply means that *stimuli generate coherent behavioral responses (and signs of clear purposeful intent, emotion, and attentional tracking)*, this metaphor of "turning on the lights" begs crucial questions about how a vast array of brainstem structures (and their connectivities) might underpin creation of conscious states. In this sense, the assumed primary functional correlate ("nonspecific arousal") may be a non-explanation. *If the extended group of reticular systems enables coherent and purposeful behaviors to emerge from the system, then it cannot simply be "turning on the lights" but must be underpinning a global integration of function of the kind Merker outlines*. The scientific challenge is now to map out this process, instead of being comfortably ensconced in an ignorance of which we are largely unaware. Without

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

more discomfort about that ignorance, we will fail to explore these questions adequately. Despite impressive gains, we know far less than we think we do.

NOTE

1. Email author for reprint of this article.

Author's Response

Grounding consciousness: The mesodiencephalon as thalamocortical base

DOI: 10.1017/S0140525X07001173

Bjorn Merker

Gamla Kyrkvagen 44, SE-14171 Segeltorp, Sweden.

gyr694c@tninet.se

Abstract: My response addresses general commentary themes such as my neglect of the forebrain contribution to human consciousness, the bearing of blindsight on consciousness theory, the definition of wakefulness, the significance of emotion and pain perception for consciousness theory, and concerns regarding remnant cortex in children with hydranencephaly. Further specific topics, such as phenomenal and phylogenetic aspects of mesodiencephalic-thalamocortical relations, are also discussed.

It was with some trepidation that I turned to the many commentaries on my target article, but the constructive tenor of collegial exchange and criticism that met me in their pages sustained me through my work on this response. Six issues recurred with sufficient frequency to merit general treatment, namely, my neglect of the forebrain contribution to human consciousness, the implications of so-called blindsight for consciousness theory, questions related to the definition and mechanisms of wakefulness, the nature of emotion and its subcortical organization, the significance of pain perception for consciousness theory, and concerns regarding remnant cortex in children with hydranencephaly. I will deal in general terms with each of these in turn before attending to additional issues on an individual basis.

R1. My deliberate neglect of the telencephalon

Considering the set of commentaries as a whole, no single issue appears to have caused more problems than my attempt to leave the forebrain on the sidelines while exploring whether any kind of phenomenal consciousness might, in fact, be implemented at brainstem levels in the absence of or without reliance upon telencephalic mechanisms. In different ways and to varying extent, a number of suggestions, questions, or objections contained in the commentaries by **Aboitiz, López-Calderón, & López** (**Aboitiz et al.**), **Barceló & Knight**, **Behrendt**, **Coenen**, **Collerton & Perry**, **Edelman**, **Freeman**, **Gilissen**, **Morin**, **Morsella & Bargh**, **Seth**, and **Watkins & Rees** concern my neglect of the obvious and massive contribution of the telencephalon to adult human consciousness. Let me assure these commentators that I harbor no greater doubts than they do about its importance in this regard. However, the topic clearly announced in the title of my target article is not that of accounting for adult human consciousness, but whether a conscious mode of function is conceivable apart from cortical mechanisms. In order to explore that question, I set out to search for grounds upon which some form of phenomenal consciousness might prove to have functional utility at more basic levels of neural organization, and if so, to try to identify neural mechanisms at the level of the brainstem that might plausibly implement such a mode of conscious function.

I found those grounds in the enhanced control economy, which I suggest can be achieved on the basis of interfacing target selection, action selection, and the ranking of needs in what I call a "selection triangle." I went on to propose that the triad of large structures physically encircling the brainstem reticular formation at the level of the midbrain, namely, the periaqueductal gray matter, the superior colliculus, and the substantia nigra (or their non-mammalian homologs/analogs), implements a vertebrate selection triangle, most particularly through a direct mutual interface of those three major midbrain components in the intermediate-to-deep (premotor, output-oriented) layers of the superior colliculus (Fig. 4 of the target article), layers which, in turn, project to the reticular formation. I suggested, moreover, that the format in which that interface is organized amounts to a conscious mode of function.

Needless to say, the phenomenal aspects of a candidate mode of conscious function implemented at that level would lack innumerable characteristics of adult human consciousness. I suggest, for example, that the "world" of its target selection domain would be devoid of three-dimensional objects, consisting instead of "a two-dimensional screen-like map of spatial directions on which potential targets might appear as mere loci of motion in an otherwise featureless noise field" (sect. 4.2, para. 10). I even suggest a concrete instantiation of such a phenomenology in the synthetic stimulus generated by Stoerig and Barth (2001). Such a visual world might appear threadbare to an adult human surrounded by the three-dimensional world supplied by his or her forebrain visual system, but it would be a visual world nevertheless. Moreover, I sketch a reason for why, even prior to forebrain expansion, *conscious* access to such a simple world might be preferable to dwelling in the dark night of unconsciousness – namely, as a means to implement the selection triangle in the form of an analog neural reality simulator – and how a system yielding such access might be structured.

My claim that the nested format proposed for the reality simulator amounts to *a conscious mode of function* (sects. 4.2 and 4.3) obviously reaches into the depths of definitional matters pertaining to consciousness, and accordingly, is unlikely to be settled in the short term. Suffice it to say that it accords well with the most global outlines of our own sensory consciousness, from whose implicit ego-center inside our body we gaze out at our world – a world that remains imperturbably stable, despite the body-based mobility of the receptor arrays which are our sole source of information about a physical universe. The key to understanding my entire proposal is this very claim, namely, that a neural arrangement which nests a body map within a world map around the origin of

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

a shared coordinate system (all three together serving economy of orienting for the fulfillment of needs) is conscious by virtue of that very arrangement itself, irrespective of its level of cognitive elaboration. This is because such an arrangement places a "subject" (the implicit perceptual ego-center under the influence of motivational bias)[1] in the presence of something other than itself (body and world, however primitively implemented), and accordingly, supplies the inherently perspectival (and asymmetric) relation which I believe supplies the principal diagnostic criterion for consciousness as such (Merker 1997).

I do not expect this claim to be taken at face value by just stating it, but it is essential to realize that the question posed in my target article is not "what is the neural organization of adult human consciousness?" but rather "might a lamprey conceivably be conscious, and if so, what might this imply for the neural organization of consciousness more generally?" Considering that, in ultimate terms, the only consciousness for which we can ever have direct evidence is our own, individual one, all such questions must of necessity be approached on indirect, circumstantial grounds. My target article accordingly arrays a highly diverse set of findings and arguments drawn from a range of disciplines spanning from comparative neurology, to behavioral neuroscience, to clinical neurology in order to sketch the outlines of at least one conceivable, if still tentative, affirmative answer to the lamprey question, and to educe some of its consequences for our conception of the neural organization of consciousness more generally.

Such a bid obviously does not amount to an account of human consciousness in full flower, let alone to a claim that its contents might "fit inside the midbrain," as it were. My target article elaborates on the far more limited aim just sketched, and by pursuing it I can hardly be faulted for neglecting the forebrain contribution to consciousness and the mechanisms that underwrite it, however important they may be in the final analysis. I have not even committed myself in the target article to an answer to the interesting and weighty question raised in the commentary by **Doesburg & Ward**: namely, to what extent, if any, the putative phenomenal content supported by an upper brainstem mechanism along the lines I sketch might, in fact, form part of the contents of normal adult human consciousness (see my response to their commentary, further on). All I have ventured to suggest is that in the absence of a cerebral cortex, and upon its prenatal loss more specifically, the brainstem might be capable of supporting a form of phenomenal consciousness on the basis of its own highly conserved and sophisticated sensory-motor-motivational circuitry.

R2. Blindsight, consciousness, and self-report

The approach just sketched would nevertheless be pointless if it could be shown that the very possibility of phenomenal consciousness were, in principle, abolished in the absence of all or some part of the telencephalic machinery. The much debated issue of how so-called blindsight might bear on consciousness theory has been interpreted by some to do just that, and because the issue was mentioned in this sense in commentaries by **Behrendt**, **Glassmann**, **Piccinini**, **Watkins & Rees**, **Schlag**, and **Doesburg & Ward**, a general comment is in order.

Blindsight refers to phenomena such as visually guided reaching and low-level visual discriminatory capacity exhibited by patients with cortical blindness caused by damage to their geniculostriate visual system. It should be clearly recognized that no mystery is attached to the basic fact that visual information may control behavior in the absence of a geniculostriate system: a number of visual systems complete paths from the retina to motor control subcortically, and others – notably the tectopulvinar system – do so by traversing extra-striate cortical paths (Goodale 1996; Ingle 1991; Weller 1988). The issue of blindsight in consciousness theory concerns which of these systems might support visual awareness and which ones do not.

If the very possibility of visual awareness were to be abolished by striate cortex lesions, then primary visual cortex would be necessary for visual consciousness, and this by extension would support a corticocentric model for consciousness more generally (though even then Sprague-effect type phenomena may complicate matters; see Pöppel and Richards 1974). This issue is controversial, and has been repeatedly reviewed (Cowey 2004; Pollen 2003; Tong 2003). We need not, however, enter into its details, because a crucial set of findings on the star patient of the blindsight research, known as GY in the literature, has radically recast the bearing of these phenomena on consciousness theory. Studies on this patient account for a disproportionate share of the blindsight literature, and for years he maintained that although he was aware of "something" during stimulus presentation in his affected visual field, it did not have the character of a visual percept. However, by asking him to match this "something" to synthetic stimuli presented in his good visual field, it has now been shown that his percept nevertheless is a distinctly visual one (Stoerig & Barth 2001).

In this patient at least, a destructive lesion of primary visual cortex has not eliminated the possibility of phenomenal visual consciousness in the affected parts of his visual field. Thus, until the blindsight phenomenon has been systematically subjected to the "matching" test, the presumption should be that blindsight phenonmena harbor no radical implications for consciousness theory. There is a further lesson for consciousness research in this development: The availability of verbal self-report in humans has been regarded as a fundamental tool and asset of consciousness research, yet here is a clear instance in which reliance upon it has vitiated the inferences drawn from exacting laboratory studies. Verbal self-report by no means provides a "gold-standard" for determining the presence or absence of awareness (a point also made by **Anand**), particularly so in the many interesting circumstances in which potential contents of consciousness are marginal, unfamiliar for a variety of reasons, degraded, or near threshold.

It would be most natural and understandable if what GY meant by a visual percept were something like a "visual object," an instance of the fully formed three-dimensional object perception for which the cortical visual system evolved, but which, of course, is not the only kind of visual experience possible. The sample of the synthetic

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

stimulus accompanying the Stoerig and Barth report is most illuminating in this regard, and is all the more interesting from the present perspective, in that the percept is of a kind that might plausibly be supported by collicular mechanisms. Note also that even a methodological advance such as that recently reported by Persaud and colleagues (Persaud et al. 2007) will have to contend with this difficulty of knowing what an experimenter's question does, in fact, mean to the person to whom it is put, a problem familiar to anthropologists. In sum, then, the evidence from studies of blindsight so far does not show that visual awareness cannot exist in the absence of visual cortex, and the phenomenon accordingly does not eliminate the possibility that such awareness might be implemented at brainstem levels.

R3. Wakefulness, responsiveness, and consciousness

The concept of wakefulness and its neural mechanisms also caused some problems, specifically in comments by **Coenen**, **Morin**, and **Piccinini**. As often happens in the technical employment of terms taken from ordinary language, the technical usage "wakefulness" does not correspond to what we normally mean when we use that word in unselfconscious speech. When we say that someone is awake, we ordinarily mean to include command of the full range of faculties that tend to become available to us when waking up in the morning, that is, seeing, hearing, volition, and conscious functioning more generally. That is not, however, the way the term is used in physiology and neurology, and particularly not when the term "wakefulness" is employed in the context most germane to our topic, namely, in the definition and diagnosis of the vegetative state (Andrews 1999). Here the usage is more specific; an individual whose eyes open as part of a functioning sleep-wake cycle is said to be awake. In order to qualify as "vegetative" this state of wakefulness must exclude consciousness. Let us, for the sake of clarity, call this state of *unconscious wakefulness* "physiological wakefulness."

In diagnosing the vegetative state one must exclude the possibility that *in addition to* being awake in this sense the patient might be conscious. The neurological tests for environmental responsiveness are motivated by this necessity. They are employed as *proxies* for consciousness in individuals belonging to a species whose conscious status is unproblematic (except in the context of certain notorious thought experiments), and who exhibit behavioral signs normally associated with consciousness (namely, an eyes-open phase in a sleep-wake cycle), but who lack the capacity for self-report because of neurological damage. Such rough and ready proxies cannot, of course, deliver a reliable verdict regarding the presence or absence of consciousness. Indeed, when clinical populations diagnosed as vegetative by their routine use are subjected to more rigorous scrutiny, erroneous diagnosis is found to be a frequent occurrence (Andrews et al. 1996; Childs et al. 1993; Tresch et al. 1991). Moreover, in overall terms, the diagnostic error exhibits a consistent direction, such that patients who are in fact conscious are more often classified as vegetative than the reverse (a circumstance of some interest in relation to the issue of consciousness in children with hydranencephaly).

This, then, is the context for my use of "awake" and "wakefulness" and "responsiveness" in the target article. I carefully avoid letting the term "awake" stand for "conscious," but I always add terms such as "seeing, hearing" or other references to *experience* when referring to a conscious mode of function. My appeal to sensory responsiveness is predicated on the clinical context outlined earlier, and it has as its background the role that is played by children with hydranencephaly in my treatment. It figures in my summary of the capacities of decorticate mammals, as well, for whom massive anatomical, physiological, and behavioral homologies support the presumption of a conscious mode of normal, waking, brain function (Seth et al. 2005). This makes the application of criteria derived from human clinical experience a reasonable approach in their case as well, at least provisionally.

That, however, does not mean that responsiveness or purposive behavior as such, and without the constraining contexts just outlined, are relevant to the assessment of the presence of consciousness. Spinal reflexes, the various tropisms, and other forms of responsiveness exhibited by plants and unicellular animals, and even nonliving systems such as thermostat-controlled central heating, should be enough to dispose of that possibility. Responsiveness certainly does not entail consciousness, but in certain clinical circumstances the presence of sensory responsiveness can move a patient from one diagnostic category to another. With that clarification, I hope to have disambiguated the usage of "wakefulness," and, in addition, to have removed any puzzlement occasioned by my treatment of responsive and purposively moving medusas as nonconscious, while at the same time suggesting that responsive and purposively moving children with hydranencephaly are conscious (**Behrendt**). In ultimate terms, the distinction between conscious and nonconscious can never be made in behavioral terms, but hinges on the presence of a functioning neural mechanism of consciousness.

R4. Emotion

The topic of feelings and emotions was mentioned in numerous commentaries, and served as the main theme of three of them, namely those of **Izard, Panksepp,** and **Van Honk, Morgan, & Schutter** (**Van Honk et al.**) It also figured more indirectly in those of **Morsella & Bargh, Northoff,** and **Watt.** In ordinary language, feelings and emotions are something one experiences, that is, they are treated as inherently conscious phenomena. As such, they are of central concern to any theory of consciousness, and were featured in the present proposal as one of the three principal domains of its selection triangle. The commentaries add a multifaceted treatment of the topic far beyond its sketchy inclusion in my target article, and the complementarity and agreement between that of Izard, focused on human data, and those with a more comparative cast, is a welcome reminder of the conserved nature of the foundations of our psychological make-up.

Each feeling/emotion "feels differently" and makes us want to do different things (Sachs 1967; see also

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Devor). This is what I mean by their role as "biases" in the economy of consciousness, so well captured in the commentary by **Izard.** His inclusion of "interest" among the emotions is well taken, and can be used to illustrate the point. It makes us want to explore. In this capacity, it is of central importance to telencephalic mechanisms of learning, memory, and problem solving, but it too has subcortical moorings. They include the hypothalamus (Swanson 2000), the midbrain dopaminergic system (see the interesting summary in the commentary by **Aboitiz et al.**; Bunzeck & Düzel 2006), the brainstem underpinnings of the navigation system (Sharp et al. 2001), and the mesopontine state control nuclei, whose important cholinergic component is highlighted in the commentary by **Collerton & Perry**.

The action-oriented content of feelings/emotions bears on the question raised by **Panksepp** regarding how we are to conceive of the first origins of conscious organization. My suggestion is that the emotional, sensory, and action aspects of consciousness were linked from the outset by providing the functional reason for a specifically conscious mode of organization. **Izard** points to the sensory occasions for emotional reactions, which, once aroused, exert their regulatory effects on behavior. The "innate releasing mechanisms" of ethology, often subcortically organized, supply a rich source of comparative evidence in this regard. **Morsella & Bargh** provide striking illustrations of how the action outcome, and the need to resolve potential conflicts between independent systems in order to achieve it, is intimately related to whether a certain process intrudes on consciousness or not. This rationale may even extend to the visceral nervous system mentioned by Panksepp, in that those aspects of it that engage consciousness would seem to be those that in one form or another require action on the body or the external world. Hunger and thirst, for example, inherently engage all three components of the selection triangle, but even a vague feeling like intestinal distress may serve to halt the further ingestion of food that may have been its cause (see Morsella & Bargh's commentary).

From these reflections on the topic of emotion addressed by these commentators, I turn to what amounts to a modality, which in a sense straddles the boundary between an emotional and a sensory system, namely, pain. In its often-accurate localizing capacity it serves a sensory function, whereas in its prepotent hedonic strength it epitomizes emotion. No other modality, save olfaction (which figures in commentaries by **Freeman** and **Morsella & Bargh**), comes even close to this inherent coupling between sensory and affective domains.

R5. Pain

Three commentaries address various aspects of the complex of theoretical, empirical, and clinical issues surrounding the perception of pain at perinatal, as well as adult stages of development (**Anand**, **Devor**, **Brusseau & Mashour**). It is gratifying to have this response from clinically oriented investigators, because no phenomenon casts the issues raised in my target article into sharper relief than the experience of pain. The reason is presumably the biological importance of the information it conveys, serving to alert an animal to a condition whose continuation would lead to tissue damage and ultimately to death. The nociceptive system is accordingly given high priority among the brain's signalling systems, a priority reflected not only in the multiple mechanisms devoted to it along the neuraxis, from spinal reflexes to cortical representation (Prescott et al. 1999), but in the hedonic strength with which it intrudes on consciousness. Overall, the pain system delivers the most powerful of the emotional-motivational "biases" governing the "needs" domain of the selection triangle I propose as the key to conscious function.

The coupling of motivational urgency (need), appropriate defensive measures (action), and swift localization of the offending source with regard to body surface and its surrounding space (target) is acute in the case of pain, and accordingly, can be expected to make an early appearance in the evolution of life forms, as well as in ontogeny (in good agreement with the evidence for prenatal pain sensitivity discussed in the commentaries). It must have helped shape the "optic brain" at the outset of vertebrate phylogeny, and today we find it prominently represented among the midbrain members of the proposed selection triangle: not only in the periaqueductal gray matter (Behbehani 1995), but in the intermediate to deep layers of the superior colliculus, as well (Bittencourt et al. 2005; McHaffie et al. 1989; Redgrave et al. 1996a; 1996b; Telford et al. 1996; Wang et al. 2000).

An upper brainstem implementation of a mechanism of primary consciousness, sketched in my target article, may thus help resolve some of the conceptual and empirical problems encumbering an exclusively corticocentric approach to the *experience* of pain so incisively presented and discussed in the commentaries. Parallels are also apparent with problems surrounding the definition and diagnosis of the vegetative state. Indeed, pain may be the Achilles' heel of this clinical entity. When, for the first time, a coma patient opens his or her eyes following a sharp cutaneous pinch, and thus clinically qualifies as having emerged into a vegetative state (assuming no additional sensory responsiveness), are those eyes opened by "an unconscious brainstem reflex"? Or does their opening signify the first fleeting emergence of the patient into consciousness, propelled into that state more readily by pain than other senses because its hedonic and arousing power exceeds that of other senses for basic biological reasons?

Such questions may be difficult to answer, but they deserve our attention, not only for reasons of basic science, but because they are fraught with consequences for medical ethics. Taken together, the three "pain commentaries" provide a many-faceted and rich treatment which brings both of these aspects of the topic into focus. They substantially add to and expand upon the perspective I have tried to articulate.

R6. Concerns about remnant cortex

The commentaries by **Coenen, Collerton & Perry, Freeman,** and **Watkins & Rees** express concerns regarding the possible role of remnant cortex in the capacities expressed by children with hydranencephaly. The target article is very clear about its presence in these children,

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

and gives a number of reasons why this factor is unlikely to provide an adequate account of their behavior. One of these is the contrast between their visual as compared to their auditory responsiveness, for which an account based on brainstem mechanisms provides a fit, whereas a cortical one does not. Here, I only wish to add that the thorough documentation and study of the capacities of these children has barely begun. My summary account is a preliminary one and in no way definitive, though it is my hope that it may provide a stimulus for the systematic kind of study that eventually will issue in a comprehensive account of their capacities, including details about what contribution, if any, spared cortex may make to those capacities. There are, moreover, children who live without any cortex at all, and some are born entirely without telencephalon (anencephaly). Their capacities too await systematic study, which will help determine the extent to which remnant cortex may play a role in hydranencephaly.

Freeman also asks about the extent of cortical removal in the studies of experimentally decorticated animals. In the studies by Whishaw and Kolb cited in my target article neocortex plus the partly allocortical cingulate gyrus was always removed. Even more extensive ablations do not necessarily alter outcomes in broad terms. Thus, the mating ability of decorticate male rats is not reduced by including the hippocampus in the removal (Whishaw & Kolb 1983), and even more radical damage, such as total removal of all telencephalic tissue, does not prevent a rat from performing and learning in an avoidance test situation (Huston & Tomaz 1986). This, of course, does not mean that decorticate animals do not have deficits (see, e.g., Whishaw et al. 1981), nor that different extents of lesions do not make a difference in outcomes. Rather, the bearing of these interventions on the topic I explore is that a basic level of differentiated and coherent behavioral competence survives even complete cortical removal.

The above six topics, then, cover my general response to over-arching concerns reflected in the commentaries. They raise numerous additional issues that deserve serious consideration. I cannot hope to cover them all in this reply, but I will attempt to deal with a set of further specific issues on an individual basis, in the hope of adding precision and perhaps removing some misapprehensions.

R7. Other specific issues

I am in perfect agreement with **Barceló & Knight**'s detailed demonstration of frontal top-down influence on the centrencephalic system. I would only add that such control is exercised "in cortical terms," that is, on the basis of cortical information, and that cortical information may not always be decisive for the global control of behavior. Let us assume that while a macaque is reaching for a manipulandum to deliver its verdict regarding a visual pattern discrimination, it suffers a sudden, sharp sting from an insect which has worked its way into the laboratory undetected. The macaque will withdraw its hand and launch defensive measures, some of which may be initiated prior to the completion of a prefrontal information path. My suggestion, far from novel (see Prescott et al. 1999, and references therein), is that some of these "early" effects engage mesodiencephalic structures served by effector paths of their own, and that frontal engagement belongs to the swift follow-up by which cortical mechanisms assess the significance of the event. The latter process would engage the entire circuitry outlined in Figure 1 of the commentary. **Barceló & Knight**'s commentary reminds us of how closely the sophisticated attainments of cortical mechanisms are tied in to the highly conserved mesodiencephalic machinery, in this case, specifically to the intermediate layers of the superior colliculus, which figure prominently in my proposal.

Issues already covered in my first three general topics repeatedly apply to **Behrendt**'s commentary. Some further matters follow here. Behrendt refers to thalamocortically dependent phenomenal contents of consciousness such as dreams and hallucinations and asks how they might relate to the brainstem systems I outline. Such contents are of course thalamocortical (see my response to **Doesburg & Ward**), but the superior colliculus is likely to be engaged under these circumstances no less than is the inferior colliculus. The superior colliculus does not remain passively open to sensory afference irrespective of stages of the sleep-wake cycle or levels of vigilance. Like the thalamocortical complex, it is yoked to sleep-wake cycles through projections from the mesopontine state control nuclei, and its unit responsiveness and intrinsic interactions are exquisitely sensitive to sleep-wake stages, as well as to levels of anesthesia, something which applies to its deeper layers in particular (for recent examples, see Brecht et al. 1999; 2001; Wang et al. 2000).

The possibility that mesodiencephalic mechanisms implement a first form of conscious function does not rob unconscious processes of places to hide. As the commentary by **Morsella & Bargh** makes clear, the cerebral cortex itself is one of these "places." The basal ganglia are another, and there is room left for them in the mesodiencephalon as well, because the structures I invoke occupy only part of that territory. Nor should the cerebellum be overlooked in this connection. The abstract diagram of my Figure 5 includes three different and bi-directional principal interfaces for unconscious activity, explicitly noted in the legend.

Behrendt misrepresents my position on the nature of the evidence for consciousness in children with hydranencephaly by joining a quote from my text to a context to which the quoted words clearly do not belong. As reference to the target article (end of 7th paragraph of sect. 5) will show, it is the "absences" of absence epilepsy in these children that I call "a weighty piece of evidence regarding their conscious status" and not their expressions of pleasure or excitement – a very different matter, indeed.

Finally, the ego-center that plays a crucial role in my scheme should not be identified with self experience, if the latter is taken in its reflective sense (see Note 1, and **Northoff**). I invoke, in this connection, a striking expression of Schopenhauer's. Reference to the page I cite will show that Schopenhauer there says exactly what I claim him to be saying. **Behrendt** is correct, however, in identifying my position regarding consciousness with that of philosophical idealism, though I prefer not to use the term on account of the history of

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

controversy, misunderstanding, and misuse with which it has been burdened.

My general comment on my neglect of the forebrain in the target article, and the comments on wakefulness, apply to **Coenen**'s commentary. Here, I only want to note that Meeren et al. (2005, cited in the target article) differ from Penfield and Jasper regarding the mechanism of absence epilepsy, principally by demonstrating that absence seizures can be *initiated* from cortical locations (something for which Penfield and Jasper had seen no evidence when stimulating the exposed cortex electrically, although other forms of seizure were thus induced; Penfield & Jasper 1954), and not with regard to the involvement of subcortical structures as such.

Besides recalling my usual caveats regarding my neglect of the forebrain, **Doesburg & Ward**'s commentary gives me the opportunity to address the issue of how one is to conceive of the relationship between a putative brainstem mechanism of primary consciousness and "thalamocortical consciousness" in *phenomenal* terms. I skirt this issue in my target article, which gives only the most rudimentary sketch of some of the circuitry that relates the two anatomically, but does not venture to suggest what might follow in phenomenal terms from that relatedness. Does any aspect of mesodiencephalic phenomenal content "show up" among the contents of adult human consciousness?

I assume, as a matter of course, that the contents of adult human consciousness are largely products of the thalamocortical complex. Considering our visual sensory consciousness alone, it is cast in the format of a panoramic three-dimensional world filled with shaped objects in complex mutual relations. The telencephalon is needed to stage such spectacles, whether one relies upon an avian "wulst" or a mammalian neocortex to gain entry to them (cf. **Edelman**). Imagine now using a clever projection system which allows one to superimpose on that scene elaborated by the forebrain an appropriately scaled midbrain rendition of the same scene. The phenomenal content of the latter, I have suggested, may resemble "mere loci of motion in an otherwise featureless noise field" (sect. 4.2, para. 10). As such, it would have nothing substantial to add to the cortical phenomenology. In fact, it might not even be detected in such a superposition, though it might be detectable by appropriate psychophysical procedures.

If for no other reason than this "dwarfing by contrast," the phenomenal content of the mesodiencephalic mechanism is unlikely to make much of a contribution to the phenomenal content of creatures equipped with a massive thalamocortical complex. Yet, as the relative size of this complex shrinks with diminishing encephalization index across mammals and beyond them into vertebrates without a neocortex, that contrast will diminish apace, with ever more of a *relative* contribution to phenomenal consciousness being made by the upper brainstem mechanism. This is my alternative to the assumption that function "migrates" from midbrain to forebrain in the course of phylogeny ("corticalization of function"), an issue discussed with reference to consciousness by Sewards and Sewards (2000). My alternative obviates a need to invoke any form of active suppression of the midbrain content of consciousness as encephalization progresses. Every function stays intact where evolution provided a neural mechanism for it; yet, as new, sophisticated mechanisms evolve, synthesizing ever more impressive "reality simulations," interest or focal awareness naturally dwells where the richest information exists. In our case, that is the forebrain, whereas for a lamprey, it is likely to be its multimodal tectum.

Given that I incline to discount a substantial contribution of midbrain content to the phenomenal content of intact, adult human conscious contents, how is one to construe the fact that at the same time I hold that the mesodiencephalic system is "integral to the constitution of the conscious state"? The issue deserves a fuller discussion than I can provide here (see also my response to **Watkins & Rees**), but in all brevity, the reason is that the tandem arrangement of zona incerta/superior colliculus is an integral part of the real-time logistics of the functional economy of the forebrain. By being tied in to the relevant higher-order nuclei of the thalamus through direct and prominent projections from both colliculus (excitatory) and zona incerta (inhibitory), this tandem arrangement is bound to affect the actual moment-to-moment composition of the contents of adult human consciousness. In light of the ubiquitous intrinsic inhibitory connectivity of the zona incerta, its role in this regard is likely to include swift and categorical decisions among rival contenders for awareness at a truly global level of gating (substrates for which are scarce in the thalamocortical complex itself, though this issue too deserves a more thorough discussion than I can provide here). In view of the midline-straddling commissural connectivity of the zona incerta stressed in the target article, this global gating should extend across the midline, a point of potential importance for our understanding of neglect syndromes ("extinction on double simultaneous stimulation"; see Bender 1952).

In sum, the circuitry is there, exerting powerful synaptic effects on the higher-order nuclei of the thalamus (Bartho et al. 2002). In view of this, it would seem that no account of the neural mechanisms responsible for the moment-to-moment composition of the contents of human consciousness can be complete without incorporating the zona incerta/superior colliculus tandem circuitry in its scheme. It intrudes directly on forebrain function, not by adding its own phenomenal contents to the forebrain's contents, but by supplying directly to the higher-order thalamus a running account of its own dual distillate of widespread convergent afference. Since the thalamic nuclei they address in push-pull fashion are those most directly tied to attention, neglect,[2] and consciousness, input from the tandem circuitry forms part of the balance of forces through which rival claims for awareness are settled, and, if my proposal has any merit, even helps settle them. I am suggesting, in other words, that the mesodiencephalic circuitry is an integral part of the function of selection in the thalamocortical complex, which **Doesburg & Ward** briefly discuss in their final paragraph. This would make the midbrain, and not the dorsal thalamus, the "base" of even the most elaborated mechanism of consciousness, in good agreement with my proposal that it is from that base that it originally expanded by the addition of ever more sophisticated circuitry from a rostral direction.

Gardner's commentary brings up a number of issues at the interface of robotics and decision theory relevant to the theoretical background of my perspective. In my

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

target article I use "optimize" in the sense of "achieve savings," rather than in any mathematically defined sense of optimality. The claim is that equipped with the selection triangle interface, an animal will achieve a more efficient deployment of its orienting behavior than would be possible in its absence. Its very purpose is efficient real-time management of the many trade-offs and compromises enforced by the multiple needs, actions, and targets that must find matches as opportunities present themselves over time in a lively and unpredictable world. With regard to the seminal contributions of Brooks it should be noted that his programmatic introduction of layered control architectures specifically excluded the kind of mechanism I propose. Among his guiding principles we find "little sensor fusion" and "no central models" (Brooks 1986, concisely summarized in Prescott et al. 1999). Massive sensor fusion is manifestly present in the superior colliculus of all vertebrates, and is incorporated directly into the "central model" of my proposed "analog reality simulator" (its analog nature setting it apart from every such model cast in the form of symbolic representation, it should be noted). The only way to introduce such a "central model" without prejudice to the considerable advantages offered by layered control is to place its nodal machinery at the highest level of the control architecture, and let its output contribute what is more akin to a bias than a command in the control of behavior, as in the present proposal. Hence, the emphasis I place on identifying what in fact constitutes the "highest level" of the vertebrate brain in control terms (rather than in cognitive ones). That, of course, does not mean that I "locate" adult human consciousness in the midbrain. What I do is to locate the "base" of the thalamocortically expanded human reality simulator in the midbrain (for which, see my response to **Doesburg & Ward**). Concerning the possibility of "*in silico* consciousness" see my concluding remarks.

Regarding **Gilissen**'s query about self-recogniton, I refer to my first and third general responses, with further details in my response to **Doesburg & Ward**. Gilissen's fascinating account of the competences of jumping spiders reminds us that analogy (similar solutions to similar selection pressures) is the companion to homology (similarity on account of shared ancestry) in the evolution of life forms. This makes it unsafe to assume that a conscious mode of function will be found only in our own evolutionary vicinity. It also tells us that the familiar relations of the vertebrate brain plan will give us little guidance when we go outside our own phylum looking for fellow conscious creatures. If my suggestion that the savings offered by the selection triangle drives the evolution of consciousness has any merit, we would nevertheless not be groping entirely in the dark when embarking on such excursions. A neural interface between action selection, target selection, and motivation, and in command of orienting, would be the first thing to look for, with scrutiny of its format coming next. Gilissen's account of jumping spiders tempts me to go looking for such an interface in a species of *Portia*, and I thank him for putting me on its trail.

Glassmann raises and alludes to so many interesting issues that a lengthy essay would be needed to cover their full sweep. Let me therefore pick out a few items only. His observation of a transient dissociation between pitch and yaw components of orienting in cats with large cortical lesions is interesting from the point of view of the centrality assigned to an intermediate spherical coordinate system for orienting responses in my treatment. He asks whether intermodal and intramodal plasticity occurs in the mesodiencephalon itself, and the answer is indeed yes. For a striking demonstration of intermodal plasticity in the tectum, see Hyde and Knudsen (2001). The issue is relevant to the question of learning in children with hydranencephaly, alluded to in my target article. The important topic of working memory and its close relation to consciousness, finally, was given far too cursory a treatment in my target article. Glassmann helps remedy this shortcoming, with additional reference to the topic being provided by **Aboitiz et al.** and **Barceló & Knight.**

Krauzlis provides a concise summary of experimental evidence bearing on a collicular role in target selection, with special reference to its causal role. Particularly useful is his careful delimitation of what we know with some assurance from still unsettled issues. One of these is the extent to which the colliculus might reflect decisions made elsewhere rather than make them itself, an issue also raised in the commentaries by **Barceló & Knight** and **Prescott & Humphries**. There is no doubt about the prominence of its nigral and frontal cortical inputs in this regard; yet, considering the vast diversity of afferents converging on the colliculus below its stratum opticum, and the richness of interactions taking place within the colliculus itself, it would seem that these sources might not always be able to determine outcomes uniquely. However, as Krauzlis points out, that is an issue on which evidence is needed, promising another installment in the unfolding story of collicular competence so well summarized in his commentary.

I have repeatedly referred to the commentary by **Morsella & Bargh,** and here I want to add only a few comments. Their concern with identifying processes within the overall economy of brain function that enter consciousness and those that do not, and what may account for the difference, is a powerful tool in coming to grips with the nature and function of consciousness. I made some halting steps in this direction in a previous publication (Merker 2005), and find the examples provided by Morsella & Bargh to be both striking and apt. The approach could be extended into the compilation of a systematic inventory of such "included" and "excluded" functions. Their suggestion to exploit timing relations is well worth pursuing. It is an interesting fact in this connection that the direct retinal projection to the colliculus and the very indirect one via lateral geniculate, visual cortex, and thence to colliculus are roughly matched in their collicular "arrival time" (Berson 1988; Waleszczyk et al. 1999). In terms of the approach more generally, I would hesitate, however, to rely directly on the more extreme of the time estimates provided by Libet (see Libet et al. 1979), on account of the problems encumbering their interpretation (Pockett 2006, provides an entry to this issue).

My general comments on deliberately neglecting the telencephalon (commissures included) and comments on the term "wakefulness" both apply to **Morin**'s commentary, but some specific errors contained in it deserve additional notice. He mistakenly asserts that my definition of consciousness excludes its self-reflective form. In my use of the Indian "scale of sentience" for definitional

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

purposes, I say that "Each 'stage' in this scale, from mere experienced sensation to self-consciousness, falls within the compass of consciousness as here defined, and presupposes it" (target article, sect. 1, para. 5). Its fourth stage reads, "So this is I who am affected by this which is so" (sect. 1, para. 4), an admirably concise formulation of self-reflective awareness. I go on to refer to animals with advanced degrees of encephalization as the likely possessors of this form of awareness. In my definition I include all possible forms of consciousness "from mere experienced sensation to self-consciousness," making this a "broad" definition, whereas Morin prefers to exclude all but its self-reflective ("full-blown") varieties from serious consideration.

Self-reflective consciousness is certainly a worthy topic of study, and if my reference to it as "akin to a luxury" seems disparaging, I apologize. But to be conscious is not necessarily to be self-conscious even in the case of adult humans, as **Morin** himself has usefully pointed out in connection with its intermittency in everyday circumstances (Morin 2006, p. 366). Moreover, by neglecting the distinctions drawn in my general comment on wakefulness and responsiveness, Morin erroneously claims that neurophysiological evidence has supported the conclusion that consciousness is possible without a cortex for quite some time now. It is only for "physiological wakefulness" that such agreement exists, a state which is a presupposition for consciousness but does not include it (see my general comment on wakefulness). It therefore falls outside the compass of my definition of consciousness.

To avoid the danger of misidentifying aspects unique to a specialized form of consciousness as generic attributes of consciousness itself, a broad sampling of valid exemplars is desirable. Moreover, a focus on "full-blown" instances raises the question "whose full-blownness?" Are we to exclude patients with global aphasia from exhibiting any awareness worth our consideration because they lack "full-blown" human consciousness, which perforce includes language competence? Better, then, to first abstract a common denominator of conscious states from their many forms (Merker 1997), and let what they share rather than what divides them inform our conception of the nature of conscious function.

As far as I can tell, **Piccinini** has understood the main lines of my proposal. With reference to his fourth paragraph, I hope that it is clear that I think that the conscious contents of children with and without hydranencephaly differ, though both are of a phenomenal kind. I do not, however, think that the distinction between them relates to the philosophical distinction between creature consciousness and state consciousness. The reason is that I think McBride (1999) was correct in pointing out that the philosophical distinction is in the nature of a grammatical difference pertaining to how we use the word "consciousness" in different situations, and does not correspond to different psychological or ontological kinds of consciousness.

Prescott & Humphries' challenging commentary gives me an opportunity to clarify some essential aspects of the "selection triangle" sketched in my proposal, because they have misread its components. These are not hypothalamus, periaqueductal gray, and colliculus, nor does the zona incerta replace the basal ganglia as the principal mechanism for action selection in my scheme. The action selection vertex of the proposed selection triangle is explicitly assigned to the basal ganglia, as follows: "The third member of the selection triangle enters this system through the prominent projections from the substania nigra to the intermediate collicular layers [refs.]. Here the final distillate of basal ganglia action-related information is interdigitated with the latticework of histochemically defined compartments that organize the input-output relations of the intermediate colliculus" (sect. 4.2 of the target article). That is, hypothalamus and periaqueductal gray are both part of the "motivation/emotion" vertex of the triangle, its action selection domain being occupied by the basal ganglia by way of the substantia nigra, with the superior colliculus itself supplying the target selection vertex.

I did not introduce the selection triangle as a mechanism for action selection, but as a mechanism of consciousness. As such, it takes the output of action selection as only one of its three principal inputs; and by interfacing the three within a unitary coordinate framework tying together ego-center, body, and world, it delivers a higher-order informational quantity (say in the form of a vector in a multidimensional space) that is added as a final optimizing bias to the global control of behavior, principally as a means of enhancing the *economy* of orienting behavior. That control – action selection included – could and perhaps would take place without it, but with a reduction (of unknown magnitude) in the efficiency of the overall deployment of orienting behavior towards the satisfaction of needs, according to my proposal.

A more precise specification of the "higher-order informational quantity" generated by the selection triangle awaits the formal modelling of the neural reality simulator, and ultimately its mathematical formalization. Presumably, dynamic interactions at the selection triangle interface are such as to define a unique location within it at each successive moment of psychological time, a location which, informally speaking, would indicate a direction of "prevailing concern or preoccupation of the moment." Such matters are, of course, not always reflected in overt behavior, which is one of the difficulties in dealing with consciousness rather than behavior. The closest that I can come to a generic characterization of its nature at this point would be "consequentiality," if one includes within the scope of that term both innate and acquired grounds for what might "matter" to an animal (for an acquired aspect, see Merker 2004a, pp. 572–73).

It is as a mechanism of selection among competing moment-to-moment bids for this hypothetical quantity that the zona incerta offers a highly suggestive connectivity, rather than for selection among actions themselves. The zona incerta adds a second external source of inhibition of collicular circuitry to that of the substantia nigra. The functional consequences of this dual external inhibition in the setting of the incompletely known complexities of intrinsic collicular circuitry are currently unknown and need to be elucidated before we can know who might dominate whom (and in what circumstances) in the intricacies of mesodiencephalic connective relations. For example, I do not think it is safe to assume that there are no conditions under which one or more of the numerous excitatory inputs converging upon the colliculus might not carry signal strengths jointly sufficient to penetrate even a combined nigral-incertal inhibitory

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

screen. It is even difficult to know whether the notion of a single hegemon is applicable to the complex dynamics animating this richly interconnected territory.

None of this, of course, casts any doubt on **Prescott & Humphries**' conclusion that "the BG [basal ganglia] are therefore ideally placed to provide the required funnel from distributed cortical processing to sequential brainstem operation." Distributed cortical processing is, however, only one of many sources of information along the neuraxis converging upon the mesodiencephalon, and according to the logic of layered control, the telencephalic level sometimes may have to resign itself to being overridden *without even being consulted* when signals regarding elemental necessities activate equally elemental brain stem (or even spinal) remedies, as illustrated by the account of the multiple levels of control governing defensive behavior offered by Prescott and colleagues (Prescott et al. 1999; see also my response to **Barceló & Knight**; in such cases the cortex is, of course, informed, but "after the fact," as it were; see Merker 2005, p. 98).

An astounding diversity of direct afferents from the entire length of the neuraxis converge on the deeper reaches of the superior colliculus, as well as on the zona incerta, both of which would seem to enjoy a truly global or "synoptic" view of CNS activity (see Edwards [1980] and references therein; Mitrofanis 2005). Let us remember, also, that the early vertebrate striatum lacked a globus pallidus and ventral tegmental area/substantia nigra output system proper. It relied instead on the nucleus tuberculi posterioris and the ventral thalamus of comparative terminology to translate its decisions into behavior (Grillner et al. 2005; Pombal et al. 1997; Smeets et al. 2000). The zona incerta of mammals is a direct derivative of this ventral thalamus, and supplies an, until recently, unsuspected source of powerful GABAergic inhibition to both thalamus and colliculus. Our understanding of functional relations among mesodiencephalic structures will remain incomplete until its contribution has been systematically charted.

Re-reading my account in the light of the commentary provided by **Prescott & Humphries,** I can see that in my target article I could have made a clearer distinction between the arguments by which I seek to establish the general point of the mesodiencephalon ("optic brain") as a nexus of superordinate control revolving around "integration for action" (not to be equated with action selection proper), on the one hand, and the additional – and conceptually distinct – discourse through which I introduce my selection triangle conception of the mechanism of consciousness, on the other. By partly assimilating the two I may have invited some of the misunderstandings I have tried to clear up here, and I thank the authors for giving me occasion to be more precise about the unique contribution I think a reality simulator cast in conscious format may make to the brain's functional economy.

The commentary by **Schlag** reminds us that mammals have (added?) collicular layers above the stratum opticum, which covers the surface of the colliculus in other vertebrates. The role of this superficial colliculus, and its relation to the deeper layers has been much debated in the past. In some ways it resembles a displaced thalamic nucleus intimately related to the posterior portion of the higher-order thalamic nuclei. But it is also connected to the deeper layers anatomically (see, e.g., Behan & Appell 1992), a connection which is functional (Doubell et al. 2003; Özen et al. 2000), and is unmasked by blocking inhibitory influences by bicuculline (Isa et al. 1998). As a direct contributor to the deeper layers, the superficial colliculus belongs to my scheme, though in agreement with Schlag's conclusion, the selection triangle interface of that scheme involves the deeper layers preferentially. I have considered the bearing of blindsight on consciousness theory in my general comments; and comments related to Schlag's suggestion regarding phylogeny in relation to hydranencephaly can be found in my response to **Doesburg & Ward.**

Seth gives a concise summary of one coherent proposal for why the unique connectivity of the cerebral cortex should be accorded a central place in the constitution of consciousness. As mentioned in my general introductory statement and in my response to **Doesburg & Ward,** I am in full agreement with assigning it such a role, as long as that role is not taken to exclude the possibility that a conscious mode of function may be implemented by other means. Naturally, when I state in the introduction of the target article that the functional utility of such an alternative implementation is independent of the sophistication with which its contents are elaborated, I mean only that it possesses functional utility, even in a rudimentary implementation, and not that increasing its sophistication would not enhance its utility.

That cortical connectivity possesses a distinctive "signature" with interesting characteristics has been revealed by measures of "mutual information" and other quantitative methods in the studies cited in **Seth's** commentary. But how are we to know that this signature provides a better fit with the characteristics of consciousness than with alternative functions, other than on intuitive grounds? We have no metric by which to assess the type of complexity possessed by consciousness, and in the absence of a quantitative method for determining "goodness of fit" between the two, alternatives might be worth considering. One such alternative is that the graph theoretic characteristics of cortical connectivity provide an optimal structure for information storage in memory, along lines I have presented in an earlier publication (Merker 2004a). In fact, the combination of differentiation with integration in cortical connectivity would seem to issue directly in that felicitous combination of item specificity with classificatory generality in memory storage, which I there propose as a unique advantage of specifically cortical connectivity. The issue seems worth exploring further.

The commentary by **Watkins & Rees** adds much valuable detail and a number of challenges. Of the latter, the ones based on blindsight may at least in part support a collicular role in awareness rather than challenge it, in light of the demonstration by Stoerig and Barth (2001) that GY is not phenomenally blind in his affected visual field (see my general comment on blindsight). That is, the collicular activity seen in connection with stimulus presentation in what was formerly referred to as GY's "blind" field may be the very neural activity that, in fact, constitutes his visual percept, though other possibilities are not at this time excluded. Since GY was also the subject for the experiment involving emotional faces cited by the commentators, the new blindsight results may affect its interpretation, as well (see commentary by **Izard**, and Reddy et al. 2006). Note, in this connection, that the

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

deeper layers of the superior colliculus receive afference from emotion-related brainstem circuitry (sect. 4.2 and Fig. 4 of the target article), an integral aspect of the selection triangle scheme.

Concerning the S-cone example, nothing I am aware of having stated implies a collicular role in which, say, direct afference from a peripheral source is a condition for its responsiveness to information supplied by that source, as if the collicular system worked in isolation prior to involvement in a change in conscious contents. On the contrary, much information reaches it indirectly, and it was above all its massive receipt of monosynaptic cortical afference, in layer upon layer throughout its depth, that I had in mind when suggesting that it supplies an essential step in the process by which one content of consciousness replaces another. It lies as an interposed filter in the path by which the descending output of layer 5 pyramidal cells returns to the cortex via the higher-order thalamic nuclei, after drastic compression in the mesodiencephalic bottleneck. It is in this position that I consider it to lie "in the loop" of a process that constitutes the contents of adult human consciousness, as discussed in my response to **Doesburg & Ward** and further on here. The direct path from cortical layer 5 to the superior colliculus is also a potential factor in conscious percepts evoked by direct electrical stimulation of the visual cortex, mentioned in the commentary.

The case reported by Weddell (2004) was cited in passing in my target article for its extension of evidence for the Sprague effect to humans. The rarity of comparable studies after neurological damage focused on the colliculi (itself rare, cf. commentary by **Schlag**) makes it important indeed, but its details are complicated. The patient exhibited a stage-wise sequence of neglect (left or right depending on stage) and other perceptual changes associated with the growth of a dorsal midbrain tumor in combination with frontocortical damage incurred during emergency shunting. In the course of its progression, the tumor invaded the thalamus, and the exact extent of collicular damage at different anatomical levels and stages of progression is unclear. Weddell's account of his findings is a tour-de-force of neurological inference, but it had to rely on numerous assumptions for which direct evidence is lacking. That said, the case provides evidence on the consequences of collicular damage, which in some respects supports the collicular role in adult human consciousness that I have suggested, and in other respects requires its revision.

It is noteworthy that the upper brainstem tumor damage exerted its primary effect on the type of forebrain functions tested in assessing neglect, which reflect competitive and selective processes in a number of ways (see, e.g., Geng & Behrmann 2006; Bender 1952). As I hope to have made clear, above all in my response to **Doesburg & Ward**, it is not by adding any conspicuous phenomenal content of its own to forebrain phenomenal consciousness that I regard the mesodiencephalic system to be integral to the constitution of even adult human consciousness, but in terms of affecting its moment-to-moment composition through just such competitive and selective processes. I refer to the special relation of the zona incerta/superior colliculus to the higher-order thalamic nuclei in this connection, and Weddell invokes the tecto-pulvinar and tecto-reticular systems in his account of the neglect findings in his patient, in agreement with what I propose.

Watkins & Rees are perfectly correct, however, in pointing out that the results of visual field perimetry in this patient run counter to my prediction that *"one conscious content will not be replaced by another without involvement of the mesodiencephalic system."* The detection of a stimulus in the perimeter involves the replacement of one conscious content by another, and, assuming that at least the colliculus was, in fact, completely disconnected from the thalamocortical complex in this patient, this replacement of conscious content would have taken place without its assistance. Since there were content replacements that did depend on collicular involvement (i.e., those constituting the patient's neglect syndrome), it seems that distinctions are necessary regarding which types of content replacement, in fact, are dependent upon the mesodiencephalic mechanism I outline. A hint in this regard is provided by the nature of perimetry, in which stimuli typically are presented singly, and thus do not require competitive selection processes – processes which lie at the heart of my conception of a selection triangle. Though further research is indicated, I am indebted to Watkins & Rees for alerting me to this need to refine my conception of the interaction between the mesodiencephalic and thalamocortical systems.

With that, I have come to the end of my comments on specific issues on an individual basis. As the attentive reader will have noticed, a considerable portion of these responses has been devoted to clarifying misapprehensions and correcting mistakes. No commentator should therefore feel slighted by not having been thus noticed. On the contrary, that is likely to indicate large areas of agreement between us. I have, however, benefited from every commentary, and thank each author for their contribution.

R8. Concluding remarks

The large number of commentaries alluding to my neglect of the forebrain illustrates the point made in my target article concerning the hold that a corticocentric perspective exercises over current thinking about consciousness. As can be seen from my reply to **Doesburg & Ward** (sect. 7, para. 8), such a perspective may even have merit in the case of adult human consciousness. My concern is that it fails to provide adequate guidance to the comparative study of consciousness, as well as to our understanding of the status of brain-damaged patients with regard to conscious function. Let me summarize, then, my position in a way that would not have been possible without the stimulation provided by the many and varied commentaries.

The corticocentric perspective can, in roughest outline, be rendered by a formula according to which the brain's mechanism of consciousness consists of "a brainstem-based system of wakefulness" (in the sense of physiological wakefulness) plus "a cortex-based system of consciousness." My sense is that this formula needs to be differentiated along two dimensions, one pertaining to systems-level organization and one to phylogeny. To begin with systems organization, I think that the brainstem contribution to consciousness is a dual one, and not single. On the one hand, it supplies an enabling function responsible for maintenance of the waking state in the sense of

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

physiological wakefulness as part of the sleep-wake cycle. This is the brainstem function I refer to in the target article as unproblematic and well-established, following the pioneering work of Moruzzi and Magoun (1949). In its modern incarnation, it consists of the mesopontine state control nulcei (adrenergic locus coeruleus, cholinergic pedunculopontine, and laterodorsal tegmental nuclei, and serotonergic dorsal raphé) plus the ascending reticular activating system (itself a complex entity, as underscored by **Watt**).

To this I would add a second brainstem function, which on its own, in the absence of cerebral cortex, may support a primary form of phenomenal consciousness. It is implemented, I suggest, in the structural complex I call the selection triangle, composed of periaqueductal gray, superior colliculus, and substantia nigra, surrounding the midbrain reticular formation. The deeper colliculus supplies a core interface between these three, in intimate interaction with the zona incerta. To this dual brainstem organization, the thalamocortical complex adds an ever more sophisticated expansion of phenomenal content over and above the upper brainstem primary mode, in accordance with the relative extent of encephalization in different vertebrates. This expansion culminates in the elaborate perceptual and cognitive contents of consciousness exhibited by highly encephalized mammals, a content which, in a few forms, includes self-consciousness (great apes and perhaps a few species of cetaceans), with humans uniquely adding language, as well.

Encephalization, then, introduces the second, phylogenetic, dimension of conceptual differentiation, in the form of the consequences that different degrees of encephalization entail for the nature of conscious contents. Some categorical differences in conscious contents, such as that between a capacity for self-consciousness and its absence, are matters intrinsic to the telencephalon, reflecting different degrees of elaboration of the thalamocortical complex, a matter that was no more than mentioned in passing in my target article. All vertebrates have a telencephalon, though of astoundingly different relative size. It follows that differences in conscious contents between different species will largely reflect differences in telencephalic organization between them. By comparison, the primary mode I suggest to be common to them all on account of highly conserved brainstem circuitry would exhibit less variation across species (compare, however, the colliculus/tectum of a tree shrew or an owl with that of a lamprey!). Regarding the relationship between the phenomenal content of the primary mode and that of the consciousness serving a highly encephalized mammal such as ourselves, see my response to **Doesburg & Ward** (sect. 7, para. 8).

At the end of this odyssey, I return to the metaphor introduced early in my target article in the form of the Indian scale of sentience. A conscious mode of function organized at the brainstem level would, I suggest, be sufficient to encompass its first two "stages," up to and including "this is so" (say, stimulus direction with respect to the animal, qualitatively different emotions and their degrees, etc.). In light of **Northoff**'s incisive analysis it might even extend into the third stage of the scale. The thalamocortical complex would cover an elaboration of its first three stages, and in some highly encephalized species, would add the fourth stage as well. At whatever stage of sophistication, these contents are coherently organized in nested fashion around an implicit ego-center supplying the origin of the nesting coordinate system – an arrangement whose format, I suggest, defines consciousness.

It is my hunch that any creature, or device for that matter, that would get about in the world as efficiently as a vertebrate without using more neural resources (or their silicon equivalent) than that vertebrate, would have to be equipped with the kind of analog reality simulator so far merely sketched in my account, but susceptible to further development in more formal terms. Thus equipped, it would be conscious, because its implicit ego-center would anchor a perspectival view coherently relating a simulated body to a simulated world. These latter entities, whether simply implemented or elaborate, and whether cast in a neural medium or eventually in silicon, are synthetic ones, contrived as efficiency measures in action control for the fulfillment of needs. It is the format, and not the medium of its implementation, that determines conscious status, I suggest.

I have learned much from my reading of the many and interesting commentaries, and from responding to them. It seems to me that by now the complete *BBS* treatment of my topic has arrived at a point where, at least, it will be difficult to misunderstand what I am in fact proposing. It gives me tremendous satisfaction to have had this opportunity for clarification, and I thank every commentary author for helping me to come to this point, and *Behavioral and Brain Sciences* for providing a forum for conducting exercises such as this.

Dedication: I dedicate my author's response to the memory of Heather Joy Krueger (18 January 2001 – 2 March 2007).

NOTES

1. This is not to be confused with self-consciousness (or reflective self-consciousness in **Northoff**'s more precise terminology, which represents a substantive advance over that employed in my target article).

2. For a recent contribution to the mechanisms of neglect relevant to the present perspective, not cited in the target article, see Rushmore et al. (2006).

References

[The letters "a" and "r" before author's initials stand for target article and response references, respectively.]

Abe, J. A. & Izard, C. E. (1999) The developmental functions of emotions: An analysis in terms of differential emotions theory. *Cognition and Emotion* 13:523–49. [CI]

Abeles, M. (1982) Role of the cortical neuron: Integrator or coincidence detector? *Israel Journal of Medical Science* 18:83–92. [aBM]

Aboitiz, F., López, V., López-Calderón, J. & Carrasco, X. (2006) Beyond Endophenotypes: An interdisciplinary approach to attentional deficit-hyperactivity disorder. In: *Focus in cognitive psychology research*, ed. M. A. Vanshevsky, pp. 110–123. Nova Science. [FA]

Adams, D. B. (1979) Brain mechanisms for offense, defense and submission. *Behavioral and Brain Sciences* 2:201–41. [aBM]

Adrian, E. D., Bremer F. & Jasper, H. H., eds. (1954) *Brain mechanisms and consciousness*. Charles C. Thomas. [aBM]

Albano, J. E. & Wurtz, R. H. (1978) Modification of the pattern of saccadic eye movements following ablation of the monkey superior colliculus. *Neuroscience Abstracts* 4:161. [aBM]

Albers, F. J. & Meek, J. (1991) Dendritic and synaptic properties of collicular neurons: A quantitative light and electron microscopical study of Golgi-impregnated cells. *Anatomical Record* 231:524–37. [aBM]

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Allport, D. A. (1987) Selection for action: Some behavioral and neurophysiological considerations of attention and action. In: *Perspectives on perception and action*, ed. H. Heuer & A. F. Sanders, pp. 395–419. Erlbaum. [aBM]

Altman, J. S. & Kien, J. (1989) New models for motor control. *Neural Computation* 1:173–83. [aBM]

An, X., Bandler, R., Öngür, D. & Price, J. L. (1998) Prefrontal cortical projections to longitudinal columns in the midbrain periaqueductal gray in macaque monkeys. *Journal of Comparative Neurology* 401:455–79. [aBM]

Anand, K. J. S. & Aynsley-Green, A. (1985) Metabolic and endocrine effects of surgical ligation of patent ductus arteriosus in the human preterm neonate: Are there implications for further improvement of postoperative outcome? *Modern Problems in Paediatrics* 23:143–57. [KJSA]

Anand, K. J. S. & Carr, D. B. (1989) The neuroanatomy, neurophysiology, and neurochemistry of pain, stress, and analgesia in newborns and children. *Pediatric Clinics of North America* 36(4):795–822. [KJSA]

Anand, K. J. S. & Craig, K. D. (1996) New perspectives on the definition of pain. *Pain* 67(1):3–6; discussion 209–11. [KJSA]

Anand, K. J. S. & Hickey, P. R. (1987) Pain and its effects in the human neonate and fetus. *New England Journal of Medicine* 317:1321–29. [aBM]

Anand, K. J. S., Rovnaghi, C., Walden, M. & Churchill, J. (1999) Consciousness, behavior, and clinical impact of the definition of pain. *Pain Forum* 8(2): 64–73. [KJSA]

Anderson, J. R. (2001) Self and others in nonhuman primates: A question of perspective. *Psychologia* 44:3–16. [EG]

Andre, M., Plenat, F., Floquet, J. & Picard, L. (1975) Major cerebral lesions with normal neonatal neurologic behavior. *Archives Francaises de Pediatrie* 32:915–24. (In French.) [aBM]

Andrews, K. (1999) The vegetative state – clinical diagnosis. *Postgraduate Medical Journal* 75:321–24. [rBM]

Andrews, K., Murphy, L., Munday, R. & Littlewood, C. (1996) Misdiagnosis of the vegetative state: Retrospective study in a rehabilitation unit. *British Medical Journal* 313:13–16. [rBM]

Ashton, H. (2002) Motivation: Reward and punishment systems. In: *The neurochemistry of consciousness*, ed. E. Perry, H. Ashton & A. Young. John Benjamins. [JvH]

Baars, B. J. (1988) *A cognitive theory of consciousness*. Cambridge University Press. [aBM, AM, JvH]

(1993) How does a serial, integrated and very limited stream of consciousness emerge from a nervous system that is mostly unconscious, distributed, parallel and of enormous capacity? In: *Theoretical and experimental studies of consciousness*, *Ciba Foundation Symposium 174*, ed. G. Bock & J. Marsh, pp. 282–90. Wiley. [aBM]

(2002) The conscious access hypothesis: Origins and recent evidence. *Trends in Cognitive Sciences* 6:47–52. [EM]

Baars, B. J., Ramsøy, T. Z. & Laureys, S. (2003) Brain, conscious experience and the observing self. *Trends in Neurosciences* 26:671–75. [aBM]

Baddeley, A. D. (1992) Consciousness and working memory. *Consciousness and Cognition* 1:3–6. [aBM]

Baerends, G. P. (1976) The functional organization of behaviour. *Animal Behaviour* 24:726–38. [aBM]

Bagchi, A. (1975) *Indian definition of mind.* Sanskrit College Research Series, No. XCVIII. Sanskrit College. [aBM]

Ballard, C. G., Court, J. A., Piggott, M., Johnson, M., O'Brien, J., McKeith, I., Holmes, C., Lantos, P., Jaros, E., Perry, R. & Perry, E. (2002) Disturbances of consciousness in Dementia with Lewy Bodies associated with alteration in nicotinic receptor binding in the temporal cortex. *Consciousness and Cognition* 11:461–74. [DC]

Bandler, R. & Keay, K. A. (1996) Columnar organization in the midbrain periaqueductal gray and the integration of emotional expression. *Progress in Brain Research* 107:285–300. [aBM]

Bandyopadhyay, S., Gonzalez-Islas, C. & Hablitz, J. J. (2005) Dopamine enhances spatiotemporal spread of activity in rat prefrontal cortex. *Journal of Neurophysiology* 93:864–72. [FA]

Barceló, F. & Knight, R. T. (2000) Dorsolateral prefrontal lesions alter the predictability and distractibility value of novel stimuli in a visual target detection task. *Society of Neuroscience Abstracts* 2: 839.11. [FB]

(in press) An information theoretic approach to context coding and entropy control in the human prefrontal cortex. *Cerebral Cortex* [FB]

Barceló, F., Escera, C., Corral, M. J. & Perianez, J. A. (2006) Task switching and novelty processing activate a common neural network for cognitive control. *Journal of Cognitive Neuroscience* 18:1734–48. [FB]

Barceló, F., Periañez, J. A. & Knight, R. T. (2002) Think differently: A brain orienting response to task novelty. *NeuroReport* 13:1887–92. [FB]

Barceló, F., Suwazono, S. & Knight, R. T. (2000) Prefrontal modulation of visual processing in humans. *Nature Neuroscience* 3:399–403. [FB]

Bard, P. (1928) A diencephalic mechanism for the expression of rage with special reference to the sympathetic nervous system. *American Journal of Physiology* 84:490–515. [aBM]

Bard, P. & Rioch, D. M. (1937) A study of four cats deprived of neocortex and additional portions of the forebrain. *Bulletin of the Johns Hopkins Hospital* 60:73–148. [WJF, aBM]

Barsalou, L. W. (2003). Situated simulation in the human conceptual system. *Language and Cognitive Processes* 18:513–62. [EM]

Bartocci, M., Bergqvist, L. L., Lagercrantz, H. & Anand, K. J. S. (2006) Pain activates cortical areas in the preterm newborn brain. *Pain* 122(1-2): 109–17. [KJSA]

Bartho, P., Freund, T. F. & Acsady, L. (2002) Selective GABAergic innervation of thalamic nuclei from zona incerta. *European Journal of Neuroscience* 16:999–1014. [arBM]

Bassett, J. P. & Taube, J. S. (2001) Neural correlates for angular head velocity in the rat dorsal tegmental nucleus. *Journal of Neuroscience* 21:5740–51. [aBM]

Basso, M. A., Powers, A. S. & Evinger, C. (1996) An explanation for reflex blink hyperexcitability in Parkinson's Disease. I. Superior colliculus. *The Journal of Neuroscience* 16:7308–17. [DC]

Basso, M. A. & Wurtz, R. H. (1997) Modulation of neuronal activity by target uncertainty. *Nature* 389:66–69. [RJK]

(1998) Modulation of neuronal activity in superior colliculus by changes in target probability. *Journal of Neuroscience* 18:7519–34. [aBM]

(2002) Neuronal activity in substantia nigra pars reticulata during target selection. *Journal of Neuroscience* 22:1883–94. [aBM]

Bastian, J. (1982) Vision and electroreception: Integration of sensory information in the optic tectum of weakly electric fish *Apteronotus albifrons*. *Journal of Comparative Physiology* 147:287–98. [aBM]

Bauer, P. J. (2006) Constructing a past in infancy: A neuro-developmental account. *Trends in Cognitive Sciences* 10:175–81. [CI]

Beach, F. A., Hebb, D. O., Morgan, C. T. & Nissen, H. W., eds. (1960) *The neuropsychology of Lashley: Selected papers of K. S. Lashley*. McGraw-Hill. [RBG]

Behan, M. & Appell, P. P. (1992) Intrinsic circuitry in the cat superior colliculus: Projections from the superficial layers. *Journal of Comparative Neurology* 315:230–43. [rBM]

Behan, M. & Kime, N. M. (1996) Intrinsic circuitry in the deep layers of the cat superior colliculus. *Visual Neuroscience* 13:1031–42. [aBM]

Behbehani, M. M. (1995) Functional characteristics of the midbrain periaqueductal gray. *Progress in Neurobiology* 46:575–605. [arBM]

Behrendt, R. P. (2003) Hallucinations: synchronisation of thalamocortical gamma oscillations underconstrained by sensory input. *Consciousness and Cognition* 12:413–51. [R-PB]

(2004) A neuroanatomical model of passivity phenomena. *Consciousness and Cognition* 13:579–609. [R-PB]

(2005) Passivity phenomena: Implications for the concept of self. *Neuro-Psychoanalysis* 7:185–207. [R-PB]

(2006) The subjectivity of the perceived world: Psychopathology and the mind-body problem from a perspective of idealism. In: *New developments in consciousness research*, ed. Vincent W. Fallio, pp. 189–209. Nova Science. [R-PB]

Beitz, A. J. (1982) The organization of afferent projections to the midbrain periaqueductal gray of the rat. *Neuroscience* 7:133–59. [aBM]

Bell, A. H., Corneil, B. D., Munoz, D. P. & Meredith, M. A. (2003) Engagement of visual fixation suppresses sensory responsiveness and multisensory integration in the primate superior colliculus. *European Journal of Neuroscience* 18: 2867–73. [aBM]

Bell, M. L. (1997) Postoperative pain management for the cognitively impaired older adult. *Seminars in Perioperative Nursing* 6(1):37–41. [KJSA]

Benatar, D. & Benatar, M. (2001) A pain in the fetus: Toward ending confusion about fetal pain. *Bioethics* 15(1):57–76. [KJSA]

Bender, M. B. (1952) *Disorders in perception.* Charles C. Thomas. [rBM]

Benevento, L. A. & Fallon, J. H. (1975) The ascending projections of the superior colliculus in the rhesus monkey (*Macaca mulatta*). *Journal of Comparative Neurology* 160:339–62. [aBM]

Benson, D. L., Isackson, P. J., Gall, C. M. & Jones, E. G. (1992) Contrasting patterns in the localization of glutamic decarboxylase and Ca^{2+}/calmodulin protein kinase gene expression in the rat central nervous system. *Neuroscience* 46:825–49. [aBM]

Benson, D. L., Isackson, P .J., Hendry, S. H. & Jones, E. G. (1991) Differential gene expression for glutamic acid decarboxylase and type II calcium-calmodulin-dependent protein kinase in basal ganglia, thalamus, and hypothalamus of the monkey. *Journal of Neuroscience* 11:1540–64. [aBM]

Berson, D. M. (1988) Retinal and cortical inputs to cat superior colliculus: Composition, convergence and laminar specificity. *Progress in Brain Research* 75:17–26. [rBM]

Berson, D. M. & McIlwain, J. T. (1983) Visual cortical input to deep layers of cat's superior colliculus. *Journal of Neurophysiology* 50:1143–55. [aBM]

Bezard, E., Dovero, S., Prunier, C., Ravenscroft, P., Chalon, S., Guilloteau D., Crossman, A. R., Bioulac, B., Brotchie, J. M. & Gross, C. E. (2001) Relationship between the appearance of symptoms and the level of nigrostriatal

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

degeneration in a progressive 1-methyl-4-phenyl-1,2,3,6-tetrahydropyridine-lesioned macaque model of Parkinson's disease. *Journal of Neuroscience* 21:6853–61. [RBG]

Binns, K. E. (1999) The synaptic pharmacology underlying sensory processing in the superior colliculus. *Progress in Neurobiology* 59:129–59. [aBM]

Bisti, S., Maffei, L. & Piccolino, M. (1972) Variations of the visual responses of the superior colliculus in relation to body roll. *Science* 175:456–57. [aBM]

Bittencourt, A. S., Nakamura-Palacios, E. M., Mauad, H., Tufik, S. & Schenberg, L. C. (2005) Organization of electrically and chemically evoked defensive behaviors within the deeper collicular layers as compared to the peri-aqueductal gray matter of the rat. *Neuroscience* 133:873–92. [arBM]

Bjursten, L.-M., Norrsell, K. & Norrsell, U. (1976) Behavioral repertory of cats without cerebral cortex from infancy. *Experimental Brain Research* 25: 115–30. [aBM]

Block, N. (1995) On a confusion about a function of consciousness. *Behavioral and Brain Sciences* 18:227–87. [AMLC, JvH]

(1996) How can we find the neural correlate of consciousness? *Trends in Neuroscience* 19(11):456–59. [GN]

(2005) Two neural correlates of consciousness. *Trends in Cognitive Sciences* 9:46–52. [CI]

Blumberg, B. (1994) Action-selection in Hamsterdam: Lessons from ethology. In: *The Third International Conference on the Simulation of Adaptative Behavior*, ed. D. Cliff, P. Husbands, J. A. Meyer & S. W. Wilson, pp. 108–17. MIT Press. [aBM]

Blumenfeld, H. & Taylor, J. (2003) Why do seizures cause loss of consciousness? *The Neuroscientist* 9:301–10. [aBM]

Boeve, B. F., Silbe, M. H. & Ferman, T. J. (2004) REM sleep behavior disorder in Parkinson's Disease and Dementia with Lewy Bodies. *Journal of Geriatric Psychiatry and Neurology* 17:146–57. [DC]

Bogen, J. E. (1995) On the neurophysiology of consciousness. Part 1: Overview. *Consciousness and Cognition* 4:52–62. [aBM]

Boivie, J., Leijon, G. & Johansson, I. (1989) Central post-stroke pain: A study of the mechanisms through analysis of the sensory abnormalities. *Pain* 37: 173–85. [MD]

Bokor, H., Frere, S. G., Eyre, M. D., Slezia, A., Ulbert, I., Luthi, A. & Acsady, L. (2005) Selective GABAergic control of higher-order thalamic relays. *Neuron* 45:929–40. [aBM]

Bradshaw, J., Saling, M., Hopwood, M., Anderson, V. & Brodtmann, A. (2004). Fluctuating cognition in dementia with Lewy bodies and Alzheimer's disease is qualitatively distinct *Journal of Neurology, Neurosurgery and Psychiatry* 75:382–87. [DC]

Braitenberg. V. & Schüz, A. (1998) *Cortex: Statistics and geometry of neuronal connectivity*, 2nd edition. Springer-Verlag. [WJF]

Brandão, M. L., Anseloni, V. Z., Pandóssio, J. E. De Araújo, J. E. & Castilho, V. M. (1999) Neurochemical mechanisms of the defensive behavior in the dorsal midbrain. *Neuroscience and Biobehavioral Reviews* 23:863–75. [aBM]

Braun, C. B. (1996) The sensory biology of the living jawless fishes: A phylogenetic assessment. *Brain, Behavior and Evolution* 48:262–76. [aBM]

Breau, L. M., Camfield, C. S., McGrath, P. J. & Finley, G. A. (2004) Risk factors for pain in children with severe cognitive impairments. *Developmental Medicine and Child Neurology* 46(6):364–71. [KJSA]

Brecht, M., Singer, W. & Engel, A. K. (1998) Correlation analysis of cortico-tectal interactions in the cat visual system. *Journal of Neurophysiology* 79: 2394–407. [aBM]

(1999) Patterns of synchronization in the superior colliculus of anesthetized cats. *The Journal of Neuroscience* 19:3567–79. [arBM]

Brecht, M., Goebel, R., Singer, W. & Engel, A. K. (2001) Synchronization of visual responses in the superior colliculus of awake cats. *NeuroReport* 12:43–47. [arBM]

Brodmann, K. (1909) *Vergleichende lokalizationslehre der grosshirnrinde*. Barth. [WJF]

Brooks, J. C., Zambreanu, L., Godinez, A., Craig, A. D. & Tracey, I. (2005) Somatotopic organisation of the human insula to painful heat studied with high resolution functional imaging. *Neuroimage* 27(1):201–209. [KJSA]

Brooks, R. A. (1986) A robust layered control system for a mobile robot. *IEEE Journal on Robotics and Automation* 2:14–23. [RAG, arBM]

(1989) A robot that walks: Emergent behaviour from a carefully evolved.network. *Neural Computation* 1:253–62. [RAG, aBM]

(1990) Elephants don't play chess. *Robotics and Autonomous Systems* 6: 3–15. [RAG]

(1991) Intelligence without representation. *Artificial Intelligence* 47: 139–59. [RAG]

(1994) Coherent behaviour from many adaptive processes. In: *From animals to animats 3: Proceedings of the Third International Conference on Simulation of Adaptive Behavior*, ed. D. Cliff, P. Husbands, J.-A. Meyer & S. W. Wilson, pp. 22–29. MIT Press. [aBM]

(2002) *Flesh and machines: How robots will change us*. Vintage. [RAG]

Brown, J. W. (1988) *The life of the mind*. Erlbaum. [SMD]

(1989) Essay on perception. In: *Neuropsychology of perception*, ed. J. W. Brown, pp. 233–56. Erlbaum. [aBM]

Brudzynski, S. M., Cruickshank, J. W. & McLachlan, R. S. (1995) Cholinergic mechanisms in generalised seizures: importance of the zona incerta. *Canadian Journal of Neurological Sciences* 22:116–20. [aBM]

Bruner, J. S., Goodnow, J. J. & Austin, G. A. (1956) *A study of thinking*. Wiley. [CI]

Buck, L. B. (2000). Smell and taste: The chemical senses. In: *Principles of neural science*, 4th edition, ed. E. R. Kandel, J. H. Schwartz & T. M. Jessell, pp. 625–47. McGraw-Hill. [EM]

Bunzeck, N. & Düzel, E. (2006) Absolute coding of stimulus novelty in the human substantia nigra/VTA. *Neuron* 51:369–79. [rBM]

Bures, J., Buresov, O. & Krivnek, J. (1974) *The mechanism and applications of Leão's spreading depression of electroencephalographic activity*. Academic Press. [WJF]

Burnett, L. R., Stein, B. E., Chaponis, D. & Wallace, M. T. (2004) Superior colliculus lesions preferentially disrupt multisensory orientation. *Neuroscience* 124:535–47. [DC]

Butler, A. B. (2000) Sensory system evolution at the origin of craniates. *Philosophical Transactions of the Royal Society (London B)* 355:1309–13. [aBM]

Butler, A. B. & Cotterill, R. M. J. (2006) Mammalian and avian neuroanatomy and the question of consciousness in birds. *Biological Bulletin* 211: 106–27. [DBE]

Butler, A. B. & Hodos, W. (1996) *Comparative vertebrate neuroanatomy: Evolution and adaptation*. Wiley-Liss. [aBM]

Cabanac, M. (1992) Pleasure: The common currency. *Journal of Theoretical Biology* 155:173–200. [aBM]

(1996) The place of behavior in physiology. In: *Handbook of physiology, environmental physiology*, ed. M. J. Fregly & C. Blatteis, pp. 1523–36. Oxford University Press. [aBM]

Cadusseau, J. & Roger, M. (1985) Afferent projections to the superior colliculus in the rat, with special attention to the deep layers. *Journal für Hirnforschung* 26:667–81. [aBM]

Campbell, D. T. (1956) Perception as substitute trial and error. *Psychological Review* 63:330–42. [RBG]

(1966) Pattern matching as an essential in distal knowing. In: *The psychology of Egon Brunswick*, ed. K. R. Hammond, pp. 81–106. Holt, Rinehart & Winston. [RBG]

(1974) Evolutionary epistemology. In: *The philosophy of Karl Popper, vol. 14, I & II: The library of living philosophers*, ed. P. A. Schilpp, pp. 413–63. Open Court. [RBG]

Carello, C. D. & Krauzlis, R. J. (2004) Manipulating intent: Evidence for a causal role of the superior colliculus in target selection. *Neuron* 43(4):575–83. [RJK, aBM]

Carpenter, R. H. S. (1991) The visual origins of ocular motility. In: *Vision and visual dysfunction. Vol 8: Eye movements*, ed. R. H. S. Carpenter, pp. 1–10. MacMillan. [aBM]

Carrive, P., Bandler, R. & Dampney, R. A. (1989) Somatic and autonomic integration in the midbrain of the unanesthetized decerebrate cat: A distinctive pattern evoked by excitation of neurones in the subtentorial portion of the midbrain periaqueductal grey. *Brain Research* 483: 251–58. [aBM]

Carroll, S. B., Grenier, J. K. & Weatherbee, S. D. (2001) *From DNA to diversity: Molecular genetics and the evolution of animal design*. Blackwell Science. [DBE]

Carter, C. S., Witt, D. M., Kolb, B. & Whishaw, I. Q. (1982) Neonatal decortication and adult female sexual behavior. *Physiology and Behavior* 29:763–66. [aBM]

Casagrande, V. A. & Diamond, I. T. (1974) Ablation study of the superior colliculus in the tree shrew (*Tupaia glis*). *Journal of Comparative Neurology* 156: 207–38. [aBM]

Cavanaugh, J. & Wurtz, R. H. (2004) Subcortical modulation of attention counters change blindness. *Journal of Neuroscience* 24(50):11236–243. [RJK, aBM]

Chalmers, D. J. (1996) *The conscious mind: In search of a fundamental theory*. Oxford University Press. [CI, GN]

Chartrand, T. L., Maddux, W. W. & Lakin, J. L. (2005) Beyond the perception-behavior link: The ubiquitous utility and motivational moderators of nonconscious mimicry. In: *The new unconscious*, ed. R. R. Hassin, J. S. Uleman & J. A. Bargh, pp. 334–61. Oxford University Press. [CI]

Childs, N. L., Mercer, W. N. & Childs, H. W. (1993) Accuracy of diagnosis of persistent vegetative state. *Neurology* 43:1465–67. [rBM]

Clancy, R. (1998) Electroencephalography in the premature and full-term infant. In: *Fetal and neonatal physiology*, ed. R. A. Poilin & W. W. Fox, pp. 2147–65. W. B. Saunders. [RRB]

Closs, S. J., Barr, B. & Briggs, M. (2004) Cognitive status and analgesic provision in nursing home residents. *British Journal of General Practice* 54(509): 919–21. [KJSA]

Clower, D. M., West, R. A., Lynch, J. C. & Strick, P. L. (2001) The inferior parietal lobule is the target of output from the superior colliculus, hippocampus, and cerebellum. *Journal of Neuroscience* 21:6283–91. [aBM]

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Coates, M. M. (2003) Visual ecology and functional morphology of Cubozoa (*Cnidaria*). *Integrative and Comparative Biology* 43:542–48. [SMD]
Coenen, A. M. L. (1995) Neuronal activities underlying the electroencephalogram and evoked potentials of sleeping and waking: Implications for information processing. *Neuroscience and Biobehavioral Reviews* 19:447–63. [AMLC]
(1998) Neuronal phenomena associated with vigilance and consciousness: From cellular mechanisms to electroencephalographic patterns. *Consciousness and Cognition* 7:42–53. [AMLC]
(1999) Similarities between deep slow wave sleep and absence epilepsy. *Sleep-Wake Research in The Netherlands* 10:99–103. [AMLC]
Coizet, V., Comoli, E., Westby, G. W. & Redgrave, P. (2003) Phasic activation of substantia nigra and the ventral tegmental area by chemical stimulation of the superior colliculus: An electrophysiological investigation in the rat. *European Journal of Neuroscience* 17:28–40. [FA]
Collerton, D., Perry, E. & McKeith, I. (2005) Why people see things that are not there: A novel Perception and Attention Deficit model for recurrent complex visual hallucinations *Behavioral and Brain Sciences* 28(6):737–94. [DC]
Collins, C. E., Lyon, D. C. & Kaas, J. H. (2005) Distribution across cortical areas of neurons projecting to the superior colliculus in New World monkeys. *Anatomical Record* (Part A) 285A:619–27. [aBM]
Comoli, E., Coizet, V., Boyes, J., Bolam, J. P., Canteras, N. S., Quirk, R. H., Overton, P. G. & Redgrave, P. (2003) A direct projection from superior colliculus to substantia nigra for detecting salient visual events. *Nature Neuroscience* 6:974–80. [FA]
Corbetta, M. (1998) Frontoparietal cortical networks for directing attention and the eye to visual locations: Identical, independent, or overlapping neural systems? *Proceedings of the National Academy of Sciences USA* 95:831–38. [aBM]
Counter, S. A. (2005) Music stirred her damaged brain. *The Boston Globe, Health/Science*, March 29, 2005. Available at: http://www.boston.com/news/globe/health_science/articles/2005/03/29/music_stirred_her_damaged_brain [aBM]
Courjon, J.-H., Olivier, E. & Pélisson, D. (2004) Direct evidence for the contribution of the superior colliculus in the control of visually guided reaching movements in the cat. *Journal of Physiology* 556:675–81. [aBM]
Covington, C., Taylor, H., Gill, C., Padaliya, B., Newman, W., Smart, J. R. 3rd & Charles, P. D. (2003) Prolonged survival in hydranencephaly: A case report. *Tennesee Medicine* 96:423–24. [aBM]
Cowan, N. (2001) The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences* 24:87–185. [aBM]
Cowey, A. (2004) The 30th Sir Frederick Bartlett lecture: Fact, artefact, and myth about blindsight. *Quarterly Journal of Experimental Psychology* 57A: 577–609. [rBM]
Cox, P. H. (1999) *An initial investigation of the auditory egocenter: Evidence for a "cyclopean ear."* Doctoral dissertation, North Carolina State University, Raleigh, NC. [aBM]
Craig, A. D. (2003) Interoception: The sense of the physiological condition of the body. *Current Opinion in Neurobiology* 13(4):500–505. [KJSA]
Craig, K. D. (1997) Implications of concepts of consciousness for understanding pain behaviour and the definition of pain. *Pain Research and Management* 2(2):111–17. [KJSA]
Craik, F., Moroz, T., Moscovitch, M., Stuss, D., Winocur, G., Tulving, E. & Kapur, S. (1999) In search of the self: A positron emission tomography study. *Psychological Science* 10:26–34. [AM]
Crick, F. & Koch, C. (1998) Consciousness and neuroscience. *Cerebral Cortex* 8:97–107. [JvH]
(2003) A framework for consciousness. *Nature Neuroscience* 6:119–26. [aBM, JvH]
Crutcher, M. D., Branch, M. H. DeLong, M. R. & Georgopoulos, A. P. (1980) Activity of zona incerta neurons in the behaving primate. *Society for Neuroscience Abstracts* 6:676. [aBM]
Cuevas, K., Rovee-Collier, C. & Learmonth, A. E. (2006) Infants form associations between memory representations of stimuli that are absent. *Psychological Science* 17:543–49. [CI]
Cunningham, N. (1998) Comments on Derbyshire, PAIN, 67 (1996) 210–211 [letter; comment]. *Pain* 74(1):102–106. [KJSA]
(1999) Inclusion of the nonverbal patient: A matter of moral emergency. *Pain Forum* 8:110–12. [KJSA]
Damasio, A. R. (1994) *Descartes' error*. G. P. Putnam. [JP, JvH]
(1999) *Feeling of what happens: Body, emotion, and the making of consciousness*. Harcourt Brace. [JvH, DFW]
Danober, L., Deransart, C., Depaulis, A., Vergnes, M. & Marescaux, C. (1998) Pathophysiologic mechanisms of genetic absence epilepsy in the rat. *Progress in Neurobiology* 55:27–57. [aBM]
Davis, M. & Whalen, P. J. (2001) The amygdala: Vigilance and emotion. *Molecular Psychiatry* 6:13–43. [JvH]
Dean, P., Porrill, J. & Stone, J. V. (2002) Decorrelation control by the cerebellum achieves oculomotor plant compensation in simulated vestibulo-ocular reflex. *Proceedings of the Royal Society of London, Series B* 269:1895–904. [aBM]
(2004) Visual awareness and the cerebellum: Possible role of decorrelation control. In: *The roots of visual awareness*, ed. C. A. Heywood, A. D. Milner & C. Blakemore. *Progress in Brain Research* 144:61–75. [aBM]
Dean, P. & Redgrave, P. (1984) Superior colliculus and visual neglect in rat and hamster. III. Functional implications. *Brain Research Reviews* 8: 155–63. [aBM]
Dean, P., Redgrave, P. & Westby, G. M. W. (1989) Event or emergency – 2 response systems in the mammalian superior colliculus. *Trends in Neurosciences* 12:137–47. [aBM]
DeCasper, A. J. & Fifer, W. P. (1980) Of human bonding: Newborns prefer their mothers' voices. *Science* 208:1174–76. [CI]
Delfour, F. & Marten, K. (2001) Mirror image processing in three marine mammal species: Killer whales (*Orca orcinus*), false killer whales (*Pseudorca crassidens*) and California sea lions (*Zalophus californianus*). *Behavioral Processes* 53:181–90. [EG]
Denham, S. A. & Burton, R. (2003) *Social and emotional prevention and intervention programming for preschoolers*. Kluwer Academic/Plenum. [CI]
Dennett, D. C. (1991) *Consciousness explained*. Little, Brown. [AM, EM]
Denny, A. P. & Behari, M. (1999) Motor fluctuations in Parkinson's disease *Journal of the Neurological Sciences* 165:18–23. [DC]
Denny-Brown, D. (1962) The midbrain and motor integration. *Proceedings of the Royal Society of Medicine* 55:527–38. [aBM]
Denton, D. (2006) *The primordial emotions: The dawning of consciousness*. Oxford University Press. [JP]
Deransart, C., Le-Pham, B.-T., Hirsch, E., Marescaux, C. H., & Depaulis, A. (2001) Inhibition of the substantia nigra suppresses absences and clonic seizures in audiogenic rats, but not tonic seizures: Evidence for seizure specificity of the nigral control. *Neuroscience* 105:203–11. [aBM]
Derbyshire, S. W. G. (2006) Can fetuses feel pain? *British Medical Journal* 332:909–12. [KJSA]
Derbyshire, S. W. G. & Furedi, A. (1996) Do fetuses feel pain? "Fetal pain" is a misnomer. *British Medical Journal* 313(7060):795. [KJSA]
Devlin, A. M., Cross, J. H., Harkness, W., Chong, W. K., Harding, B., Vargha-Khadem, F. & Neville, B. G. R. (2003) Clinical outcomes of hemispherectomy for epilepsy in childhood and adolescence. *Brain* 126:556–66. [aBM]
Dommett, E., Coizet, V., Blaha, C. D., Martindale, J., Lefebvre, V., Walton, N., Mayhew, J. E., Overton, P. G. & Redgrave, P. (2005) How visual stimuli activate dopaminergic neurons at short latency. *Science* 307:1476–79. [FA]
Dorris, M. C. & Munoz, D. P. (1998) Saccadic probability influences motor preparation signals and time to saccadic initiation. *Journal of Neuroscience* 18(17):7015–26. [RJK]
Dostrovsky, J. O. (2000) Role of thalamus in pain. *Progress in Brain Research* 129:245–57. [MD]
Doubell, T. P., Skaliora, I., Baron, J. & King, A. J. (2003) Functional connectivity between the superficial and deeper layers of the superior colliculus: An anatomical substrate for sensorimotor integration. *The Journal of Neuroscience* 23:6596–607. [arBM]
Dretske, F. (1993) Conscious experience. *Mind* 102:1–21. [aBM]
Driver, J. & Vuilleumier, P. (2001) Perceptual awareness and its loss in unilateral neglect and extinction. *Cognition* 79:39–88. [aBM]
Durmer, J. S. & Rosenquist, A. C. (2001) Ibotenic acid lesions in the pedunculopontine region result in recovery of visual orienting in the hemianopic cat. *Neuroscience* 106:765–81. [aBM]
Eccles, J. C., ed. (1966) *Brain and conscious experience*. Springer Verlag. [aBM]
Edelman, D. B., Baars, B. J. & Seth, A. K. (2005) Identifying the hallmarks of consciousness in non-mammalian species. *Consciousness and Cognition* 14(1):169–87. [DC, DBE, AKS]
Edelman, G. M. (2003) Naturalizing consciousness: A theoretical framework. *Proceedings of the National Academy of Sciences USA* 100(9):5520–24. [AKS]
(2006) Second nature: The transformation of knowledge. In: *Second nature: Brain science and human knowledge*, ed. G. M. Edelman, pp. 142–57. Yale University Press. [CI]
Edelman, G. M. & Tononi, G. (2000) *A universe of consciousness: How matter becomes imagination*, 1st edition. Basic Books. [DBE, AKS]
Edwards, S. B. (1980) The deep layers of the superior colliculus: Their reticular characteristics and organization. In: *The reticular formation revisited*, ed. A. Hobson & M. A. B. Brazier, pp. 193–209. Raven Press. [arBM]
Edwards, S. B., Ginsburgh, C. L., Henkel, C. K. & Stein, B. E. (1979) Sources of subcortical projections to the superior colliculus in the cat. *Journal of Comparative Neurology* 184:309–29. [aBM]
Eibl-Eibesfeldt, I. (1975) *Ethology: The biology of behavior*, 2nd edition, trans. E. Klinghammer. Holt, Rinehart & Winston. [RBG]
Eimer, M., Hommel, B. & Prinz, W. (1995) S-R compatibility and response selection. *Acta Psychologica* 90:301–23. [EM]

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Endo, T., Yanagawa, Y., Obata, K. & Isa, T. (2005) Nicotinic acetylcholine receptor subtypes involved in facilitation of GABAergic inhibition in mouse superficial superior colliculus. *Journal of Neurophysiology* 94:3893–902. [DC]

Engel, A. K, Fries, P., König, P., Brecht, M. & Singer, W. (1999) Temporal binding, binocular rivalry, and consciousness. *Consciousness and Cognition* 8: 128–51. [aBM]

Engel, A. K. & Singer, W. (2001) Temporal binding and the neural correlates of sensory awareness. *Trends in Cognitive Sciences* 5(1):16–25. [aBM, SMD]

Erickson, R. P. (1984) On the neural bases of behavior. *American Scientist* 251:233–41. [RAG]

Erickson, R. P., Di Lorenzo, P. M. & Woodbury, M. A. (1994) Classification of taste responses in the brain stem: Membership in fuzzy sets. *Journal of Neurophysiology* 71:2139–50. [RAG]

Erzurumlu, R. S. & Jhaveri, S. (1990) Thalamic axons confer a blueprint of the sensory periphery onto the developing rat somatosensory cortex. *Brain Research. Developmental Brain Research* 56(2):229–34. [KJSA]

Ewert, J.-P. (1968) Der Einfluss von Zwischenhirndefekten auf die Visuomotorik im Beutefang- und Fluchtverhalten der Erdkröte (*Bufo bufo L.*). *Zeitschrift für Vergleichende Physiologie* 61:41–70. [aBM]

Fecteau, J. H. & Munoz, D. P. (2006) Salience, relevance, and firing: A priority map for target selection. *Trends in Cognitive Sciences* 10:382–90. [aBM]

Feldt, K. S., Ryden, M. B. & Miles, S. (1998) Treatment of pain in cognitively impaired compared with cognitively intact older patients with hip-fracture. *Journal of the American Geriatric Society* 46(9):1079–85. [KJSA]

Felleman, D. J. & Van Essen, D. C. (1991) Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex* 1:1–47. [aBM]

Fernandez de Molina, A. & Hunsperger, R. W. (1962) Organization of the subcortical system governing defense and flight reactions in the cat. *Journal of Physiology* 160:200–13. [aBM]

Ferrell, B. A., Ferrell, B. R. & Rivera, L. (1995) Pain in cognitively impaired nursing home patients. *Journal of Pain and Symptom Management* 10(8):591–98. [KJSA]

Fessard, A. E. (1954) Mechanisms of nervous integration and conscious experience. In: *Brain mechanisms and consciousness*, ed. E. D. Adrian, F. Bremer & H. H. Jasper, pp. 200–36. Blackwell. [aBM]

Ficalora, A. S. & Mize, R. R. (1989) The neurones of the substantia nigra and the zona incerta which project to the cat superior colliculus are GABA immunoreactive: A double label study using GABA immunocytochemistry and lectin retrograde transport. *Neuroscience* 29:567–81. [aBM]

Findlay, J. M. & Walker, R. (1999) A model of saccade generation based on parallel processing and competitive inhibition. *Behavioral and Brain Sciences* 22: 661–74. [aBM]

Fisk, N. M., Gitau, R., Teixeira, J. M., Giannakoulopoulos, X., Cameron, A. D. & Glover, V. A. (2001) Effect of direct fetal opioid analgesia on fetal hormonal and hemodynamic stress response to intrauterine needling. *Anesthesiology* 95(4):828–35. [KJSA]

Fitzgerald, M. (2005) The development of nociceptive circuits. *Nature Reviews Neuroscience* 6(7):507–20. [KJSA]

Floyd, N. S., Price, J. L., Ferry, A. T., Keay, K. A. & Bandler, R. (2000) Orbitomedial prefrontal cortical projections to distinct longitudinal columns of the periaqueductal gray in the rat. *Journal of Comparative Neurology* 422: 556–78. [aBM]

Forster, M. C., Pardiwala, A. & Calthorpe, D. (2000) Analgesia requirements following hip fracture in the cognitively impaired. *Injury* 31(6):435–36. [KJSA]

Freeman, W. J. (2006) Definitions of state variables and state space for brain-computer interface. Part 1: Multiple hierarchical levels of brain function. *Cognitive Neurodynamics* 1(1):1871–3080 (print), 1871–4099 (Online). Available at: http://dx.doi.org/10.1007/s11571-006-9001-x [WJF]

Friede, R. L. (1989) *Developmental neuropathology*, pp. 31–39. Springer-Verlag. [aBM]

Friedman, D., Cycowicz, Y. M. & Gaeta, H. (2001) The novelty P3: An event-related brain potential (ERP) sign of the brain's evaluation of novelty. *Neuroscience and Biobehavioral Reviews* 25:355–73. [FB]

Fries, W. (1984) Cortical projections to the superior colliculus in the macaque monkey: A retrograde study using horseradish peroxidase. *Journal of Comparative Neurology* 230:55–76. [aBM]

Friston, K. (2005) A theory of cortical responses. *Philosophical Transactions of the Royal Society of London, B: Biological Sciences* 360:815–36. [FB]

Fritsch, B., Sonntag, R., Dubuc, R., Ohta, Y. & Grillner, S. (1990) Organization of the six motor nuclei innervating the ocular muscles in lamprey. *Journal of Comparative Neurology* 294:491–506. [aBM]

Fujishiro, H., Umegaki, H., Isojima, D., Akatsu, H., Iguchi, A. & Kosaka, K. (2006) Depletion of cholinergic neurons in the nucleus of the medial septum and the vertical limb of the diagonal band in dementia with Lewy bodies. *Acta Neuropathologica (Berlin)* 111:109–14. [DC]

Fuster, J. M. (1997) *The prefrontal cortex: Anatomy, physiology, and neuropsychology of the frontal lobes.* Lippincott-Raven. [FB]

Gallistel, C. R. (1999) Coordinate transformations in the genesis of directed action. In: *Cognitive science*, ed. B. O. M. Bly & D. E. Rummelhart, pp. 1–42. Academic Press. [aBM]

Gamper, E. (1926) Bau und Leistungen eines menschlichen Mittelhirnwesen (Arhinencephalie mit Encephalocele). *Zeitschrift für die gesamte Neurologie und Psychiatrie* 102:154–235, and 104: 49–120. [aBM]

Gardner, J. L. & Lisberger, S. G. (2002) Serial linkage of target selection for orienting and tracking eye movements. *Nature Neuroscience* 29:29. [RJK]

Gardner, R. A. & Gardner, B. T. (1998) *The structure of learning: From sign stimuli to sign language.* Erlbaum. [RAG]

Gawryszewski, L. G., Carreiro, L. R. R. & Magalhães, F. V. (2005) Early and late inhibitions elicited by a peripheral visual cue on manual response to a visual target: Are they based on Cartesian coordinates? *Psicológica* 26:121–37. [aBM]

Gaymard, B., Francois, C., Ploner, C. J., Condy, C. & Rivaud-Pechoux, S. (2003) A direct prefrontotectal tract against distractibility in the human brain. *Annals of Neurology* 53:542–45. [FB]

Gazzaniga, M. S. (2005) Forty-five years of split-brain research and still going strong. *National Review of Neuroscience* 6(8):653–59. [AM]

Gehring, W. J. (2005) New perspectives on eye development and the evolution of eyes and photoreceptors. *Journal of Heredity* 96:171–84. [DBE]

Geng, J. J. & Behrmann, M. (2006) Competition between simultaneous stimuli modulated by location probability in hemispatial neglect. *Neuropsychologia* 44:1050–60. [rBM]

Ghazanfar, A. A. & Schroeder, C. E. (2006) Is neocortex essentially multisensory? *Trends in Cognitive Science* 10:278–85. [EM]

Gibbs, F. A., Gibbs, E. L. & Lennox, W. G. (1937) Epilepsy: A paroxysmal cerebral dysrhythmia. *Brain* 60:377–88. [aBM]

Gibbs, F. A., Lennox, W. G. & Gibbs, E. L. (1936) Localizable features of the electrical activity of the brain in petit mal epilepsy. *American Journal of Physiology* 116:61. [aBM]

Gigerenzer, G., Todd, P. M. & the ABC Research Group (1999) *Simple heuristics that make us smart*. Oxford University Press. [RAG]

Gioanni, Y., Gioanni, H. & Mitrovic, N. (1991) Seizures can be triggered by stimulating non-cortical structures in the quaking mutant mouse. *Epilepsy Research* 9:19–31. [aBM]

Giolli, R. A.; Gregory, K. M., Suzuki, D. A., Blanks, R. H., Lui, F. & Betelak, K. F. (2001) Cortical and subcortical afferents to the nucleus reticularis tegmenti pontis and basal pontine nuclei in the macaque monkey. *Visual Neuroscience* 18:725–40. [aBM]

Glassman, R. B. (1970) Cutaneous discrimination and motor control following somatosensory cortical ablations. *Physiology and Behavior* 5:1009–19. [RBG]

(1983) Dissociation of vertical and horizontal components of somesthetic orientation-localization during recovery from cortical damage: Implication regarding central associative functions. *Physiological Psychology* 11:47–53. [RBG]

(1985) Parsimony in neural representations: Generalization of a model of spatial orientation ability. *Physiological Psychology* 13:43–47. [RBG]

(1994) Behavioral specializations of SI and SII cortex: A comparative examination of the neural logic of touch in rats, cats, and other mammals. *Experimental Neurology* 125:134–41. [RBG]

(1999) A working memory "theory of relativity": Elasticity over temporal, spatial, and modality ranges conserves 7 ± 2 item capacity in radial maze, verbal tasks, and other cognition. *Brain Research Bulletin* 48:475–89. [RBG]

(2002) "Miles within millimeters" and other awe-inspiring facts about our "mortarboard" human cortex. *Zygon/Journal of Religion and Science* 37: 255–77. [RBG]

(2003). Hypothesized temporal and spatial code properties for a moment's working memory capacity: Brain wave "harmonies" and "four-color" topology of activated cortical areas. In: *Time and mind II: Information processing perspectives*, ed. H. Helfrich, pp. 161–83. Hogrefe & Huber. [RBG]

Glassman, R. B. & Smith, A. (1988) Neural spare capacity and the concept of diaschisis: Functional and evolutionary models. In: *Brain injury and recovery: Theoretical and controversial issues*, ed. S. Finger, T. LeVere, C. R. Almli & D. G. Stein, pp. 45–69. Plenum Press. [RBG]

Glenberg, A. M. (1997) What memory is for. *Behavioral and Brain Sciences* 20:1–55. [EM]

Glimcher, P. W. & Sparks, D. L. (1992) Movement selection in advance of action in the superior colliculus. *Nature* 355(6360):542–45. [RJK, aBM]

Glover, V. & Fisk, N. (1996) We don't know: Better to err on the safe side from midgestation. *British Medical Journal* 313:796. [KJSA]

Goldberg, H. M., II. & Malach, R. (2006) When the brain loses its self: Prefrontal inactivation during sensorimotor processing. *Neuron* 50:329–39. [AM]

Goldman-Rakic, P. S. & Nauta, W. J. (1976) Autoradiographic demonstration of a projection from prefrontal association cortex to the superior colliculus in the rhesus monkey. *Brain Research* 116:145–49. [FB]

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Goldstein, L. B. & Simel, D. L. (2005) Is this patient having a stroke? *Journal of the American Medical Association* 293:2391–402. [DC]
Goltz, F. L. (1892) Der hund ohne grosshirn. Siebente Abhandlun, ber die verrichtungen des grosshirns. *Pflügers Archiv* 51:570–614. [WJF]
Goodale, M. A. (1996) Visuomotor modules in the vertebrate brain. *Canadian Journal of Physiology and Pharmacology* 74:390–400. [rBM]
Goodale, M. A. & Murison, R. C. C. (1975) The effects of lesions of the superior colliculus on locomotor orientation and the orienting reflex in the rat. *Brain Research* 88:243–61. [aBM]
Gordon, N. S., Kollack-Walker, S., Akil, H. & Panksepp, J. (2002) Expression of c-fos gene activation during rough and tumble play in juvenile rats. *Brain Research Bulletin* 57:651–59. [aBM]
Goto, M., Canteras, N. S., Burns, G. & Swanson, L. W. (2005) Projections from the subfornical region of the lateral hypothalamic area. *Journal of Comparative Neurology* 493:412–38. [aBM]
Graf, W., Gerrits, N., Yatim-Dhiba, N. & Ugolini, G. (2002) Mapping the oculomotor system: The power of transneuronal labeling with rabies virus. *European Journal of Neuroscience* 15:1557–62. [aBM]
Graybiel, A. M. (1978) A stereometric pattern of distribution of acetylthiocholinesterase in the deep layers of the superior colliculus. *Nature* 272: 539–41. [aBM]
Greenfield, S. A. (2000) *The private life of the brain.* Pergamon Press. [JvH]
Greenough, W. T. (1991) Experience as a component of normal development: Evolutionary considerations. *Developmental Psychology* 2714–17. [CI]
Gregory, R. L. (1970) *The intelligent eye*. McGraw-Hill. [RBG]
(1978) *Eye and brain*, 3rd edition. World University Library. [RBG]
Grillner, S. (2003) The motor infrastructure: From ion channels to neuronal networks. *Nature Reviews, Neuroscience* 4:573–86. [aBM]
Grillner, S., Georgopoulos, A. P. & Jordan, L. M. (1997) Selection and initiation of motor behavior. In: *Neurons, networks, and motor behavior*, ed. P. S. G. Stein, S. Grillner, A. I. Selverson & D. G. Stuart, pp. 1–19. MIT Press. [aBM]
Grillner, S., Hellgren, J., Menard, A., Saitoh, K. & Wikstrom, M. A. (2005) Mechanisms for selection of basic motor programs – roles for the striatum and pallidum. *Trends in Neurosciences* 28:364–70. [rBM]
Grobstein, P. (1988) Between the retinotectal projection and directed movement: Topography of a sensorimotor interface. *Brain, Behavior and Evolution* 31:34–48. [aBM]
(1989) Organization in the sensorimotor interface: A case of increased resolution. In: *Visuomotor coordination*, ed. J.-P. Ewert & M. A. Arbib, pp. 537–68. Plenum Press. [aBM]
Groenewegen, H. J. (2003) The basal ganglia and motor control. *Neural Plasticity* 10:107–20. [aBM]
Grofova, I., Ottersen, O. P. & Rinvik, E. (1978) Mesencephalic and diencephalic afferents to the superior colliculus and periaqueductal gray substance demonstrated by retrograde axonal transport of horseradish peroxidase in the cat. *Brain Research* 146:205–20. [aBM]
Groh, J. M. & Sparks, D. L. (1996) Saccades to somatosensory targets. III. Eye-dependent somatosensory activity in primate superior colliculus. *Journal of Neurophysiology* 75:439–53. [aBM]
Grunau, R. V. & Craig, K. D. (1987) Pain expression in neonates: Facial action and cry. *Pain* 28(3):395–410. [KJSA]
Guillaume, A. & Pélisson, D. (2001) Gaze shifts evoked by electrical stimulation of the superior colliculus in the head-unrestrained cat. II. Effect of muscimol inactivation of the caudal fastigial nucleus. *European Journal of Neuroscience* 14:1345–59. [aBM]
Gurney, K., Prescott, T. J., Wickens, J. & Redgrave, P. (2004) Computational models of the basal ganglia: From membranes to robots. *Trends in Neurosciences* 27:453–59. [TJP]
Haber, S. N. & Fudge, J. L. (1997) The primate substantia nigra and VTA: Integrative circuitry and function. *Critical Reviews in Neurobiology* 11: 323–42. [aBM]
Haberly, L. B. (1998). Olfactory cortex. In: *The synaptic organization of the brain*, 4th edition, ed. G. M. Shepherd, pp. 377–416. Oxford University Press. [EM]
Haft, M. (1998) Robust "topological" codes by keeping control of internal redundancy. *Physical Review Letters* 81:4016–19. [aBM]
Halsey, J. (1987) Hydranencephaly. In: *Handbook of clinical neurology*, ed. P. Vinken, G. Bruyn & H. Klawans, pp. 337–53. Elsevier Science. [SW]
Hamani, C., Sakabe, S., Bortolotto, Z. A., Cavalheiro, E. A. & Mello, L. (1994) Inhibitory role of the zona incerta in the pilocarpine model of epilepsy. *Epilepsy Research* 49:73–80. [aBM]
Hameroff, S. R. (2006) The entwined mysteries of anesthesia and consciousness. *Anesthesiology* 105:400–12. [RRB]
Han, C. J., O'Tuathaigh, C. M., van Trigt, L., Quinn, J. J., Fanselow, M. S., Mongeau, R., Koch, C. & Anderson, D. J. (2003) Trace but not delay fear conditioning requires attention and the anterior cingulate cortex. *Proceedings of the National Academy of Sciences USA* 100:13087–92. [aBM]
Han, Z. Y., Zoli, M., Cardona, A., Bourgeois, J. P., Changeux, J. P. & Le Novere, N. (2003) Localization of [3H]nicotine, [3H]cytisine, [3H]epibatidine, and [125I]alpha-bungarotoxin binding sites in the brain of *Macaca mulatta*. *Journal of Comparative Neurology* 461:49–56. [DC]
Harding, D. E. (1961) *On having no head*. Arkana. [aBM]
Harland, D. P. & Jackson, R. R. (2000) "Eight-legged cats" and how they see: A review of recent research on jumping spiders (*Araneae Salticidae*). *Cimbebasia* 16:231–40. [EG]
Harting, J. K., Feig, S & Van Lieshout, D. P. (1997) Cortical somatosensory and trigeminal inputs to the cat superior colliculus: Light and electron microscopic analyses. *Journal of Comparative Neurology* 388:313–26. [aBM]
Harting, J. K., Huerta, M. F., Frankfurter, A. J., Strominger, N. L. & Royce, G. J. (1980) Ascending pathways from the monkey superior colliculus: An autoradiographic analysis. *Journal of Comparative Neurology* 192: 853–82. [aBM]
Harting, J. K., Updyke, B. V. & Van Lieshout, D. P. (1992) Corticotectal projections in the cat: Anterograde transport studies of twenty-five cortical areas. *Journal of Comparative Neurology* 328:379–414. [aBM]
Hartline, P. H., Kass, L. & Loop, M. S. (1978) Merging of modalities in the optic tectum: Infrared and visual integration in rattlesnakes. *Science* 199:1225–29. [aBM]
Hassin, R. R., Uleman, J. S. & Bargh, J. A. (2005) *The new unconscious*. Oxford University Press. [CI]
Haynes, J. D., Deichmann, R. & Rees, G. (2005) Eye-specific effects of binocular rivalry in the human lateral geniculate nucleus. *Nature* 438(7067):496–99. [SW]
Heath, R. G. (1975) Brain function and behavior: I. Emotion and sensory phenomena in psychotic patients and in experimental animals. *Journal of Nervous and Mental Disease* 160:159–75. [aBM]
Hembree, E. A. (1986) Individual differences and developmental changes in infants' emotion expressions during early mother-infant interaction: Unpublished manuscript, University of Delaware. [CI]
Hepper, P. G. & Shahidullah, S. (1994) The beginnings of mind – evidence from the behavior of the fetus. *Journal of Reproductive and Infant Pscyhology* 12:143–54. [KJSA]
Hering, E. (1879/1942) *Spatial sense and movements of the eye*, trans. C. A. Radde. American Academy of Optometry. (Original work published in 1879). [aBM]
Herrick, C. J. (1948) *The brain of the tiger salamander*. University of Chicago Press. [WJF]
Hess, W. R. (1954) *Das Zwischenhirn. Syndrome, Lokalisationen, Funktionen*, 2nd edition. Benno Schwabe. [aBM]
(1957) *The functional organization of the diencephalon.* Grune & Stratton. [JP]
Hess, W. R. & Brugger, M (1943) Das subkortikale Zentrum der affektiven Abwehrreaktion. *Helvetica Physiologica Acta* 1:33–52. [aBM]
Hess, W. R., Bürgi, S. & Bucher, V. (1946) Motorische Funktion des tektal- und tegmentalgebietes. *Monatschrift für Psychiatrie und Neurologie* 112: 1–52. [aBM]
Hikosaka, O., Takikawa, Y. & Kawagoe, R. (2000) Role of the basal ganglia in the control of purposive saccadic eye movements. *Physiological Review* 80: 953–78. [TJP]
Hikosaka, O. & Wurtz, R. H. (1983) Visual and oculomotor functions of monkey substantia nigra pars reticulata. I. Relation of visual and auditory responses to saccades. *Journal of Neurophysiology* 49:1230–53. Elsevier. [aBM]
(1989) The basal ganglia. In: *The neurobiology of saccadic eye movements*, ed. R. H. Wurts & M. E. Goldberg, pp. 257–81. Elsevier. [aBM]
Hinson, J. M., Whitney, P., Holben, H. & Wirick, A. K. (2006) Affective biasing of choices in gambling task decision making. *Cognitive, Affective and Behavioral Neurosciences* 6:190–200. [JP]
Hirai, T., Onodera, S. & Kawamura, K. (1982) Cerebellotectal projections studied in cats with horseradish peroxidase or tritiated amino acids axonal transport. *Experimental Brain Research* 48:1–12. [aBM]
Hodgson, S. H. (1878) *The philosophy of reflection*. Longmans, Green. [aBM]
Hofer, M. A. (1994) Cardiac respiratory function during sudden prolonged immobility in wild rodents. *Psychosomatic Medicine* 32:633–47. [JvH]
Hoffman, J. & Liss, L. (1969) "Hydranencephaly". A case report with autopsy findings in a 7-year-old girl. *Acta Paediatrica Scandinavica* 58: 297–300. [aBM]
Holland, P. W. H., Garcia-Fernández, J., Williams, N. A. & Sidow, A. (1994) Gene duplication and the origins of vertebrate development. *Development* (Suppl.):125–33. [aBM]
Holland, L. Z. & Holland, N. D. (1999) Chordate origins of the vertebrate central nervous system. *Current Opinion in Neurobiology* 9:596–602. [aBM]
(2001) Evolution of neural crest and placodes: *Amphioxus* as a model for the ancestral vertebrate? *Journal of Anatomy* 199:85–98. [aBM]
Holstege, J. C. (1991) Ultrastructural evidence for GABAergic brain stem projections to spinal motoneurons in the rat. *Journal of Neuroscience* 11: 159–67. [aBM]

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Holstege, G., Bandler, R. & Saper, C. B., eds. (1996) *The emotional motor system.* Elsevier. [aBM]

Holstege, G. & Cowie, R. J. (1989) Projections from the rostral mesencephalic reticular formation to the spinal cord. An HRP and autoradiographical tracing study in the cat. *Experimental Brain Research* 75:265–79. [aBM]

Holstege, G. & Georgiadis, J. R. (2004) The emotional brain: neural correlates of cat sexual behavior and human male ejaculation. *Progress in Brain Research* 143:39–45. [aBM]

Holzman, R. S. & Hickey, P. R. (2001) The development of pain perception and the stress response. In: *Pediatric anesthesia in the Harvard Electronic Anesthesia Library*, ed. M. T. Bailin. Lippincott Williams and Wilkins. [RRB]

Hommel, B., Müsseler, J., Aschersleben, G. & Prinz, W. (2001) The theory of event coding: A framework for perception and action planning. *Behavioral and Brain Sciences* 24:849–937. [EM]

Horgas, A. L. & Tsai, P. F. (1998) Analgesic drug prescription and use in cognitively impaired nursing home residents. *Nursing Research* 47(4):235–42. [KJSA]

Horowitz, G. D. & Newsome, W. T. (1999) Separate signals for target selection and movement specification in the superior colliculus. *Science* 284:1158–61. [aBM]

Horowitz, S. S., Blanchard, J. & Morin, L. P. (2005) Medial vestibular connections with the hypocretin (orexin) system. *Journal of Comparative Neurology* 487:127–46. [aBM]

Horvitz, J. C. (2000) Mesolimbocortical and nigrostriatal dopamine responses to salient non-reward events. *Neuroscience* 96:651–56. [aBM]

Houk, J. C. (1991) Red nucleus: Role in motor control. *Current Opinion in Neurobiology* 1:610–15. [aBM]

Hovda, D. A. & Villablanca, J. R. (1990) Sparing of visual field perception in neonatal but not adult cerebral hemispherectomized cats. Relationship with oxidative metabolism of the superior colliculus. *Behavioral Brain Research* 39:119–32. [aBM]

Howard, I. P. & Templeton, W. B. (1966) *Human spatial orientation*. Wiley. [aBM]

Humphries, M. D., Gurney, K. & Prescott, T. J. (2006) The brainstem reticular formation is a small-world, not scale-free, network. *Proceedings of the Royal Society, B. Biological Sciences* 273:503–11. [TJP]

(in press) Is there a brainstem substrate for action selection? *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences.* [TJP, AKS]

Hunsperger, R. W. (1956) Affektreaktionen auf elektrische reizung im Hirnstamm der Katze. *Helvetica Physiologica Acta* 14:70–92. [aBM]

(1963) Comportements affectifs provoqués par la stimulation électrique du tronc cérébral et du cerveau antérieur. *Journal de Physiologie* 55:45–97. [aBM]

Hunsperger, R. W. & Bucher, V. M. (1967) Affective behaviour produced by electrical stimulation in the forebrain and brainstem of the cat. *Progress in Brain Research* 27:103–27. [aBM]

Husserl, E. (1991) *On the phenomenology of the consciousness of internal time (1893–1917)*, trans. J. Barnett Brough. Kluwer Academic. [GN]

Huston, J. P. & Tomaz, C. (1986) Subtelencephalic locale of reinforcement and learning: looking for the minimal necessary structures. *Behavioural Brain Research* 22:153–61. [rBM]

Hyde, P. S. & Knudsen, E. I. (2001) A topographic instructive signal guides the adjustment of the auditory space map in the optic tectum. *Journal of Neuroscience* 21:8586–93. [rBM]

Hydranencephaly Group Survey (2003) Unpublished questionnaire survey of 81 families conducted by Barb Aleman from September 2002 through February 2003. Available at: http://hydranencephaly.com/researchresults.htm [aBM]

Iacono, R. P. & Nashold, B. S., Jr. (1982) Mental and behavioral effects of brain stem and hypothalamic stimulation in man. *Human Neurobiology* 1: 273–79. [aBM]

Illing, R.-B. (1992) Association of efferent neurons to the compartmental architecture of the superior colliculus. *Proceedings of the National Academy of Sciences USA* 89:10900–904. [aBM]

Illing, R.-B. & Graybiel, A. M. (1986) Complementary and non-matching afferent compartments in the cat's superior colliculus: Innervation of the acetylcholinesterase-poor domain of the intermediate gray layer. *Neuroscience* 18: 373–94. [aBM]

Ingle, D. J. (1973) Two visual systems in the frog. *Science* 181:1053–55. [aBM]

(1991) Functions of subcortical visual systems in vertebrates and the evolution of higher visual mechanisms. In: *Evolution of the eye and visual system*, ed. J. R. Cronly-Dillon & R. L. Gregory, pp. 152–64. CRC Press. [rBM]

Isa, T., Endo, T. & Saito, Y. (1998) The visuo-motor pathway in the local circuit of the rat superior colliculus. *Journal of Neuroscience* 18:8496–504. [rBM]

Isa, T. & Kobayashi, Y. (2004) Switching between cortical and subcortical sensorimotor pathways. *Progress in Brain Research* 143:299–305. [aBM]

Isa, T. & Sasaki, S. (2002) Brainstem control of head movements during orienting: Organization of the premotor circuits. *Progress in Neurobiology* 66: 205–41. [aBM]

Iwahori, N., Kawawaki, T. & Baba, J. (1999) Neuronal organization of the optic tectum in the river lamprey, *Lampetra japonica*: A Golgi study. *Journal für Hirnforschung* 39:409–24. [aBM]

Izard, C. E. (1990) The substrates and functions of emotions feelings: William James and current emotion theory. *Personality and Social Psychology Bulletin* 16:626–35. [CI]

(1991) *The psychology of emotions*. Plenum Press. [CI]

(2002) Translating emotion theory and research into preventive interventions. *Psychological Bulletin* 128:796–824. [CI]

(2007) Basic emotions, natural kinds, emotion schemas, and a new paradigm. Unpublished manuscript. [CI]

Izard, C. E., Fantauzzo, C. A., Castle, J. M., Haynes, O. M., Rayias, M. F. & Putnam, P. H. (1995) The ontogeny and significance of infants' facial expressions in the first 9 months of life. *Developmental Psychology* 31: 997–1013. [CI]

Izard, C. E., Hembree, E. A. & Huebner, R. R. (1987) Infants' emotion expressions to acute pain: Developmental change and stability of individual differences. *Developmental Psychology* 23:105–13. [CI]

Jackson, J. H. (1958) Evolution and dissolution of the nervous system. In: *Selected writings of John Hughlings Jackson*, ed. J. Taylor, pp. 45–118. Stapes Press. [JvH]

Jackson, S. R., Newport, R., Mort, D. & Husain, M. (2005) Where the eye looks, the hand follows: Limb-dependent magnetic misreaching in optic ataxia. *Current Biology* 15:42–46. [aBM]

Jacobs, L. F. (1994) Natural space-use patterns and hippocampal size in kangaroo rats. *Brain, Behavior and Evolution* 44:125–32. [WJF]

James, W. (1890) *The principles of psychology*, vol. *I.* Dover. [R-PB]

(1890/1950) *The principles of psychology: Vol. 2.* Dover. [CI]

(1890/1983) *The principles of psychology*, with introduction by G. A. Miller. Harvard University Press. [aBM]

Jasper, H. H. & Droogleever-Fortuyn, J. (1947) Experimental studies on the functional anatomy of petit mal epilepsy. *Proceedings of the Association for Research in Nervous and Mental Disease* 26:272–98. [aBM]

Jasper, H. H., Proctor, L. D., Knighton, R. S., Noshay, W. C. & Costello, R. T., eds. (1958) *Reticular formation of the brain. Henry Ford Hospital International Symposium*. Little, Brown. [aBM]

Jay, M. F. & Sparks, D. L. (1987) Sensorimotor integration in the primate superior colliculus. II. Coordinates of auditory signals. *Journal of Neurophysiology* 57:35–55. [aBM]

Jennett, B. (2002) *The vegetative state. Medical facts, ethical and legal dilemmas.* Cambridge University Press. [aBM]

Jesberger, J. A. & Richardson, J. S. (1985) Animal models of depression: Parallels and correlates to severe depression in humans. *Biological Psychiatry* 20: 764–84. [WJF]

Jiang, H., Stein, B. E. & McHaffie, J. G. (2003) Opposing basal ganglia processes shape midbrain visuomotor activity bilaterally. *Nature* 423:982–86. [aBM]

Johansson, R. S., Westling, G., Bäckström, A. & Flanagan, J. R. (2001) Eye-hand coordination in object manipulation. *Journal of Neuroscience* 21: 6917–32. [aBM]

Johnson, S. C., Baxter, L. C., Wilder, L. S., Piper, J. G., Heiserman, J. E. & Prigatano, G. P. (2002) Neural correlates of self-reflection. *Brain* 125: 1808–14. [AM]

Johnston, C. C., Collinge, J. M., Henderson, S. J. & Anand, K. J. S. (1997) A cross-sectional survey of pain and pharmacological analgesia in Canadian neonatal intensive care units. *Clinical Journal of Pain* 13(4):308–12. [KJSA]

Jones, E. G. (1998) A new view of specific and nonspecific thalamocortical connections. In: *Consciousness: At the frontiers of neuroscience*, ed. H. H. Jasper, L. Descarries, V. F. Castelluci & S. Rossignol. In Series: *Advances in Neurology* 77:49–73. Elsevier. [aBM]

(2002) Thalamic circuitry and thalamocortical synchrony. *Philosophical Transactions of the Royal Society, London, Series B* 357:1659–73. [aBM]

Jones, R. M. & France, T. D. (1978) Electrophysiological responses in hydranencephaly. *American Journal of Ophthalmology* 85:478–84. [aBM]

Jordan, L. M. (1998) Initiation of locomotion in mammals. *Annals of the New York Academy of Sciences* 860:83–93. [aBM]

Julesz, B. (1971) *Foundations of cyclopean perception*. University of Chicago Press. [aBM]

Jurgens, U. (1994) The role of the periaqueductal grey in vocal behaviour. *Behavioral Brain Research* 62:107–17. [aBM]

Kaada, B. R. (1951) Somato-motor, autonomic and electrocorticographic responses to electrical stimulation of rhinencephalic and other structures in primates, cat, and dog: A study of responses from the limbic, subcallosal, orbito-insular, piriform and temporal cortex, hippocampus-fornix and amygdala. *Acta Physiologica Scandinavica (Suppl.)* 24:1–262. [aBM]

Karten, H. J. (1997) Evolutionary developmental biology meets the brain: The origins of mammalian cortex (commentary). *Proceedings of the National Academy of Sciences USA* 94:2800–804. [DBE]

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Kawamura, K. & Konno, T. (1979) Various types of corticotectal neurons of cats as demonstrated by means of retrograde axonal transport of horseradish peroxidase. *Experimental Brain Research* 35:161–75. [aBM]

Kawato, M., Hayakawa, H. & Inui, T. (1993) A forward-inverse optics model of reciprocal connections between visual cortical areas. *Network: Computation in Neural Systems* 4:415–22. [aBM]

Keay, K. A. & Bandler, R. (2002) Distinct central representations of inescapable and escapable pain: Observations and speculation. *Experimental Physiology* 87:275–79. [aBM]

Keenan, J. P., Wheeler, M. A., Gallup, Jr., G. G. & Pascual-Leone, A. (2000) Self-recognition and the right prefrontal cortex. *Trends in Cognitive Sciences* 4:338–44. [EG]

Keller, E. L., Lee, K.-M. & McPeek, R. M. (2005) Readout of higher-level processing in the discharge of superior colliculus neurons. *Annals of the New York Academy of Sciences* 1039:1–11. [aBM]

Kendrick, K. M., Hinton, M. R. & Baldwin, B. A. (1991) GABA release in the zona incerta of the sheep in response to the sight and ingestion of food and salt. *Brain Research* 550:165–68. [aBM]

Kim, U., Gregory, E. & Hall, W. C. (1992) Pathway from the zona incerta to the superior colliculus in the rat. *Journal of Comparative Neurology* 321: 555–75. [aBM]

Kipersztok, O. & Patterson, J. C. (1995) Intelligent fuzzy control to augment the scheduling capabilities of network queuing systems. *Computer Science Lecture Notes, vol. 949*. Springer-Verlag: [RAG]

Kittelberger, J. M., Land, B. R. & Bass, A. H. (2006) The midbrain periaqueductal gray and vocal patterning in a teleost fish. *Journal of Neurophysiology* 96: 71–85. [aBM]

Kjaer, T. W., Novak, M. & Lou, H. C. (2002) Reflective self-awareness and conscious states: PET evidence for a common midline parietofrontal core. *NeuroImage* 17:1080–86. [AM]

Klier, E. M., Wang, H. & Crawford, J. D. (2001) The superior colliculus encodes gaze commands in retinal coordinates. *Nature Neuroscience* 4:627–32. [aBM]

Knight, R. T. & Scabini, D. (1998) Anatomic bases of event-related potentials and their relationship to novelty detection in humans. *Journal of Clinical Neurophysiology* 15:3–13. [FB]

Koch, C. & Tsuchiya, N. (2007) Attention and consciousness: Two distinct brain processes. *Trends in Cognitive Science* 11:16–22. [FA]

Koh, J. L., Fanurik, D., Harrison, R. D., Schmitz, M. L. & Norvell, D. (2004) Analgesia following surgery in children with and without cognitive impairment. *Pain* 111(3):239–244. [KJSA]

Kolb, B. & Tees, C., eds. (2000) *The cerebral cortex of the rat*. MIT Press. [JP]

Kolmac, C. I., Power, B. D. & Mitrofanis, J. (1998) Patterns of connections between zona incerta and brainstem in rats. *Journal of Comparative Neurology* 396:544–55. [aBM]

König, P., Engel, A. K. & Singer, W. (1996) Integrator or coincidence detector? The role of the cortical neuron revisited. *Trends in Neurosciences* 19: 130–37. [aBM]

Körding, K. P. & Wolpert, D. M. (2006) Bayesian decision theory in sensorimotor control. *Trends in Cognitive Sciences* 10:319–26. [aBM]

Kosko, B. (1993) *Fuzzy thinking: The new science of fuzzy logic*. Hyperion. [RAG]

Kostovic, I. & Rakic, P. (1990) Developmental history of the transient subplate zone in the visual and somatosensory cortex of the macaque monkey and human brain. *Journal of Comparative Neurology* 297:441–70. [RRB]

Kozloski, J., Hamzei-Sichani, F. & Yuste R. (2001) Stereotyped position of local synaptic targets in neocortex. *Science* 293:868–72. [aBM]

Krauzlis, R. J. (2001) Extraretinal inputs to neurons in the rostral superior colliculus of the monkey during smooth-pursuit eye movements. *Journal of Neurophysiology* 86:2629–33. [aBM]

Krauzlis, R. J., Basso, M. A. & Wurtz, R. H. (1997) Shared motor error for multiple eye movements. *Science* 276(5319):1693–95. [RJK]

(2000) Discharge properties of neurons in the rostral superior colliculus of the monkey during smooth-pursuit eye movements. *Journal of Neurophysiology* 84(2):876–91. [RJK]

Krauzlis, R. J. & Dill, N. (2002) Neural correlates of target choice for pursuit and saccades in the primate superior colliculus. *Neuron* 35(2):355–63. [RJK]

Krauzlis, R .J., Liston, D. & Carello, C. D. (2004) Target selection and the superior colliculus: Goals, choices and hypotheses. *Vision Research* 44: 1445–51. [aBM]

Kuypers, H. G. J. M. (1982) A new look at the organization of the motor system. *Progress in Brain Research* 57:381–403. [aBM]

(1987) Some aspects of the organization of the output of the motor cortex. In: *Motor areas of the cerebral cortex, Ciba Foundation Symposium, 132*, ed. G. Bock, M. O'Connor & J. Marsh, pp. 63–82. Wiley. [aBM]

Kuypers, H. G. J. M. & Martin, G. F., eds. (1982) *Anatomy of descending pathways to the spinal cord. Progress in Brain Research, vol. 57*. Elsevier Biomedical. [aBM]

Lacalli, T. C. (1996) Landmarks and subdomains in the larval brain of *Branchiostoma:* Vertebrate homologs and invertebrate antecedents. *Israel Journal of Zoology* 42:S131–46. [aBM]

(2001) New perspectives on the evolution of protochordate sensory and locomotory systems, and the origin of brains and heads. *Philosophical Transactions of the Royal Society of London, B* 356:1565–72. [aBM]

Laemle, L. K. (1983) A Golgi study of cell morphology in the deep layers of the human superior colliculus. *Journal für Hirnforschung* 24:297–306. [aBM]

Lambie, J. A. & A. J. Marcel (2002) Consciousness and the varieties of emotion experience: A theoretical framework. *Psychological Review* 109(2): 219–59. [GN]

Lamme, V. A. F. & Spekreijse, H. (2000) Modulations of primary visual cortex activity represent attentive and conscious scene perception. *Frontiers in Bioscience* 5:232–43. [aBM]

Land, M. F. (1974) A comparison of the visual behavior of a predatory arthropod with that of a mammal. In: *Invertebrate neurons and behavior*, ed. C. A. G. Wiersma, pp. 341–431. MIT Press. (Originally published in *The Neurosciences: Third Study Program*, pp. 411–18; same year). [EG]

Lang, C. E. & Schieber, M. H. (2003) Differential impairment of individuated finger movements in humans after damage to the motor cortex or the corticospinal tract. *Journal of Neurophysiology* 90:1160–70. [aBM]

Langer, T. P. & Lund, R. D. (1974) The upper layers of the superior colliculus of the rat: A Golgi study. *Journal of Comparative Neurology* 158:418–35. [aBM]

Larkum, M. E., Senn, W. & Lüscher, H.-R. (2004) Top-down dendritic input increases the gain of layer 5 pyramidal neurons. *Cerebral Cortex* 14: 1059–70. [aBM]

Lavallée, P., Urbain, N., Dufresne, C., Bokor, H., Acsady, L. & Deschenes, M. (2005) Feedforward inhibitory control of sensory information in higher-order thalamic nuclei. *Journal of Neuroscience* 25:7489–98. [aBM]

Lawrence, D. G. & Kuypers, H. G. J. M. (1968) The functional organization of the motor system in the monkey. I. The effects of bilateral pyramidal lesions. *Brain* 91:1–14. [aBM]

LeDoux, J. E. (1996) *The emotional brain: The mysterious underpinnings of emotional life*. Simon & Schuster. [CI, EM]

(2002) *The synaptic self*. Viking. [JvH]

Lee, H. W., Hong, S. B., Seo, D. W., Tae, W. S. & Hong, S. C. (2000) Mapping of functional organization in human visual cortex: Electrical cortical stimulation. *Neurology* 54(4):849–54. [SW]

Lee, P. H., Helms, M. C., Augustine, G. J. & Hall, W. C. (1997) Role of intrinsic synaptic circuitry in collicular sensorimotor integration. *Proceedings of the National Academy of Sciences USA* 94:13299–304. [aBM]

Lee, S. J., Ralston, H. J. P., Drey, E. A., Partridge, J. C. & Rosen, M. A. (2005) Fetal pain: A systematic multidisciplinary review of the evidence. *Journal of the American Medical Association* 294(8):947–54. [KJSA]

Leh, S. E., Johansen-Berg, H. & Ptito, A. (2006) Unconscious vision: New insights into the neuronal correlate of blindsight using diffusion tractography. *Brain* 129(Pt 7):1822–32. [SMD, SW]

Lehar, S. (2002) *The world in your head: A gestalt view of the mechanism of conscious experience*. Erlbaum. [aBM]

Leichnetz, G. R., Gonzalo-Ruiz, A., DeSalles, A. A. & Hayes, R. L. (1987) The origin of brainstem afferents of the paramedian pontine reticular formation in the cat. *Brain Research* 422:389–97. [aBM]

Lewis, M., Sullivan, M. W. & Michalson, L. (1983) The cognitive-emotional fugue. In: *Emotions, cognition, and behavior*, ed. C. E. Izard, J. Kagan & R. Zajonc, pp. 264–88. Cambridge University Press. [CI]

Libet, B. (1973) Electrical stimulation of cortex in human subjects, and conscious sensory aspects. In: *Handbook of sensory physiology, vol. II*, ed. A. Iggo, pp. 743–90. Springer-Verlag. [MD]

(1986) Unconscious cerebral initiative and the role of conscious will in voluntary action. *Behavioral and Brain Sciences* 8:529–66. [EM]

(2005) *Mind time: The temporal factor in consciousness*. Harvard University Press. [EM]

Libet, B., Wright, E. W., Jr., Feinstein, B. & Pearl, D. K. (1979) Subjective referral of the timing for a conscious sensory experience: A functional role for the somatosensory specific projection system in man. *Brain* 102:193–224. [rBM]

Lippa, C. F., Smith, T. W. & Perry, E. (1999) Dementia with Lewy bodies: Choline acetyltransferase parallels nucleus basalis pathology. *Journal of Neural Transmission* 106:525–35. [DC]

Liston, D. & Krauzlis, R. J. (2003) Shared response preparation for pursuit and saccadic eye movements. *Journal of Neuroscience* 23(36):11305–14. [RJK]

(2005) Shared decision signal explains performance and timing of pursuit and saccadic eye movements. *Journal of Vision* 5(9): 678–89. [RJK]

Llinas, R. R. & Pare, D. (1991) Of dreaming and wakefulness. *Neuroscience* 44:521–35. [R-PB]

Llinas, R. R. & Ribary, U. (1993) Coherent 40-Hz oscillation characterizes dream state in humans. *Proceedings of the National Academy of Sciences USA* 90:2078–81. [R-PB]

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Lloyd-Thomas, A. R. & Fitzgerald, M. (1996) Do fetuses feel pain? Reflex responses do not necessarily signify pain. *British Medical Journal* 313(7060):797–98. [KJSA]

Lomber, S. G. & Payne, B. R. (1996) Removal of two halves restores the whole: Reversal of visual hemineglect during bilateral cortical and collicular inactivation in the cat. *Visual Neuroscience* 13:1143–56. [aBM]

Lomber, S. G., Payne, B. R. & Cornwell, P. (2001) Role of the superior colliculus in analyses of space: Superficial and intermediate layer contributions to visual orienting, auditory orienting, and visuospatial discriminations during unilateral and bilateral deactivations. *Journal of Comparative Neurology* 441:44–57. [aBM]

Lonstein, J. S., Simmons, D. A. & Stern, J. M. (1998) Functions of the caudal periaqueductal gray in lactating rats: kyphosis, lordosis, maternal aggression, and fearfulness. *Behavioral Neuroscience* 112:1502–18. [aBM]

Loop, M. S. & Sherman, S. M. (1977) Visual discriminations of cats with cortical and tectal lesions. *Journal of Comparative Neurology* 174:79–88. [SMD, aBM]

Lott, I. T., McPherson, D. L. & Starr, A. (1986) Cerebral cortical contributions to sensory evoked potentials: Hydranencephaly. *Electroencephalography and Clinical Neurophysiology* 64:218–23. [aBM]

Lundqvist, D. & Ohman, A. (2005) Emotion regulates attention: The relation between facial configurations, facial emotion, and visual attention. *Visual Cognition* 12:51–84. [CI]

Lynch, J. C., Hoover, J. E. & Strick, P. L. (1994) Input to the primate frontal eye field from the substantia nigra, superior colliculus, and dentate nucleus demonstrated by transneuronal transport. *Experimental Brain Research* 100:181–86. [aBM]

Lyon, D. C., Nassi, J. J. & Callaway, E. M. (2005) Disynaptic connections from the superior colliculus to cortical area MT revealed through transynaptic labeling with rabies virus (Abstract). *Journal of Vision* 5:432a. Available at: http://journalofvision.org/5/8/432/ [aBM]

Ma, T. P. (1996) Saccade-related omnivectoral pause neurons in the primate zona incerta. *Neuroreport* 7:2713–16. [aBM]

Ma, T. P., Cheng, H. W., Czech, J. A. & Rafols, J. A. (1990) Intermediate and deep layers of the macaque superior colliculus: A Golgi study. *Journal of Comparative Neurology* 295:92–110. [aBM]

MacLean, P. D. (1990) *The triune brain in evolution: Role in paleocerebral functions*. Plenum Press. [JP, JvH]

Maes, P. (1990) Situated agents can have goals. In: *Designing autonomous agents*, ed. P. Maes, pp. 49–70. MIT Press. [aBM]

Magoun, H. W. (1954) The ascending reticular systrem and wakefulness. In: *Brain mechanisms and consciousness*, ed. E. D. Adrian, F. Bremer & H. H. Jasper, pp. 1–20. Blackwell. [aBM]

Malviya, S., Voepel-Lewis, T., Tait, A., Merkel, S., Lauer, A., Munro, H., Farley, F. (2001) Pain Management in children with and without cognitive impairment following spine fusion surgery. *Paediatric Anaesthesia* 11(4):453. [KJSA]

Mana, S. & Chevalier, G. (2002) The fine organization of nigro-collicular channels with additional observations of their relationships with acetylcholinesterase in the rat. *Neuroscience* 106:357–74. [aBM]

Mandler, G. A. (1975) Consciousness: Respectable, useful, and *probably* necessary. In: *Information processing and cognition: The Loyola Symposium*, ed. R. Solso, pp. 229–54. Erlbaum. [aBM, AM]

(2002) *Consciousness recovered. Psychological functions and origins of conscious thought*. John Benjamins. [aBM]

Manger, P. R. (2006) An examination of cetacean brain structure with a novel hypothesis correlating thermogenesis to the evolution of a big brain. *Biological Review* 81:293–338. [EG]

Marin-Padilla, M. (1997) Developmental neuropathology and impact of perinatal brain damage. II: White matter lesions of the neocortex. *Journal of Neuropathology and Experimental Neurology* 56:219–35. [aBM]

Mashour, G. A. (2006) Integrating the science of consciousness and anesthesia. *Anesthesia and Analgesia* 103:975–82. [DC]

Masino, T. (1992) Brainstem control of orienting movements: Intrinsic coordinate system and underlying circuitry. *Brain, Behavior and Evolution* 40:98–111. [aBM]

Masino, T. & Grobstein, P. (1989) The organization of descending tectofugal pathways underlying orienting in the frog, Rana pipiens. I. Lateralization, parcellation, and an intermediate spatial representation. *Experimental Brain Research* 75:227–44. [aBM]

Masino, T. & Knudsen, E. I. (1990) Horizontal and vertical components of head movement are controlled by distinct neural circuits in the barn owl. *Nature* 345:434–37. [aBM]

Maskos, U., Molles, B. E., Pons, S., Besson, M., Guiard, B. P., Guilloux J. P., Evrard, A., Cazala, P., Cormier, A., Mameli-Engvall, M., Dufour, N., Cloez-Tayarani, I., Bemelmans, A. P., Mallet, J., Gardier, A. M., David, V., Faure, P., Granon, S. & Changeux, J. P. (2005) Nicotine reinforcement and cognition restored by targeted expression of nicotinic receptors. *Nature* 436:103–107. [aBM]

Mather, J. A. (in press) Cephalopod consciousness: Behavioural evidence. *Consciousness and Cognition*. [DBE]

May, P. J. (2005) The mammalian superior colliculus: Laminar structure and connections. *Progress in Brain Research* 151:321–78. [aBM]

May, P. J., Hartwich-Young, R., Nelson, J., Sparks, D. L. & Porter, J. D. (1990) Cerebellotectal pathways in the macaque: Implications for collicular generation of saccades. *Neuroscience* 36:305–24. [aBM]

May, P. J., Sun, W. & Hall, W. C. (1997) Reciprocal connections between the zona incerta and the pretectum and superior colliculus of the cat. *Neuroscience* 77:1091–14. [aBM]

Mazzola, L., Isnard, J. & Mauguiere, F. (2006) Somatosensory and pain responses to stimulation of the second somatosensory area (SII) in humans: A comparison with SI and insular responses. *Cerebral Cortex* 16:960–68. [MD]

McAbee, G. N., Chan, A. & Erde, E. L. (2000) Prolonged survival with hydranencephaly: Report of two patients and literature review. *Pediatric Neurology* 23(1):80–84. [aBM, SW]

McBride, R. (1999) Consciousness and the state/transitive/creature distinction. *Philosophical Psychology* 12:181–96. [rBM]

McCormick, D. A. & Contreras, D. (2001) On the cellular and network bases of epileptic seizures. *Annual Review of Physiology* 63:815–46. [aBM]

McFarland, D. (1965) Flow graph representation of motivational systems. *British Journal of Mathematical and Statistical Psychology* 18:25–43. [aBM]

McFarland, D. J. & Houston, A. (1981) *Quantitative ethology: The state space approach*. Pitman. [aBM]

McFarland, D. J. & Sibly, R. M. (1975) The behavioural final common path. *Philosophical Transactions of the Royal Society (London)* 270:265–93. [aBM]

McGurk, H. & MacDonald, J. (1976) Hearing lips and seeing voices. *Nature* 264:746–48. [EM]

McHaffie, J. G., Kao, C. Q. & Stein, B. E. (1989) Nociceptive neurons in rat superior colliculus: Response properties, topography, and functional implications. *Journal of Neurophysiology* 62:510–25. [rBM]

McHaffie, J. G., Norita, M., Dunning, D. D. & Stein, B. E. (1993) Corticotectal relationships: Direct and "indirect" pathways. *Progress in Brain Research* 95:139–50. [aBM]

McHaffie, J. G., Stanford, T. R., Stein, B. E., Coizet, V. & Redgrave, P. (2005) Subcortical loops through the basal ganglia. *Trends in Neurosciences* 28: 401–407. [TJP]

McPeek, R. M. & Keller, E. L. (2002) Saccade target selection in the superior colliculus during a visual search task. *Journal of Neurophysiology* 88(4): 2019–34. [RJK]

(2004) Deficits in saccade target selection after inactivation of the superior colliculus. *Nature Neuroscience* 7(7):757–63. [RJK, aBM]

Medina, L. & Reiner, A. (2000) Do birds possess homologues of primary visual, somatosensory and motor cortices? *Trends in Neurosciences* 23:1–12. [DBE]

Meeren, H., van Luijtelaar, G., Lopes da Silva, F. & Coenen, A. (2005) Evolving concepts on the pathophysiology of absence seizures: The cortical focus theory. *Archives of Neurology* 62:371–76. [AMLC, arBM]

Mellor, D. J., Diesch, T. J., Gunn, A. J. & Bennet, L. (2005). The importance of 'awareness' for understanding fetal pain. *Brain Research Reviews* 49: 455–71. [KJSA]

Melzack, R. & Wall, P. D. (1965) Pain mechanisms: A new theory. *Science* 150(699):971–79. [KJSA]

Menzel, C. (2005) Progress in the study of chimpanzee recall and episodic memory. In: *The missing link in cognition: Origins of self-reflective consciousness*, ed. H. S. Terrace & J. Metcalfe, pp. 188–224. Oxford University Press. [AM]

Meredith, M. A. & King, A. J. (2004) Spatial distribution of functional superficial–deep connections in the adult ferret superior colliculus. *Neuroscience* 128:861–70. [aBM]

Meredith, M. A. & Ramoa, A. S. (1998) Intrinsic circuitry of the superior colliculus: Pharmacophysiological identification of horizontally oriented inhibitory interneurons. *Journal of Neurophysiology* 79:1597–602. [aBM]

Merker, B. (1980) *The sentinel hypothesis: A role for the mammalian superior colliculus*. Doctoral dissertation, Department of Psychology and Brain Science, Massachusetts Institute of Technology. [aBM]

(1997) The common denominator of conscious states: Implications for the biology of consciousness. *Cogprints Electronic Archive: Biology; Theoretical biology*. [Archives preprint.] Available at: (http://cogprints.soton.ac.uk) [arBM]

(2004a) Cortex, countercurrent context, and dimensional integration of lifetime memory. *Cortex* 40:559–76. [arBM]

(2004b) The local and the global in cortical phylogeny and function. Reply to Finlay and Lamme. *Cortex* 40:582–83. [aBM]

(2005) The liabilities of mobility: A selection pressure for the transition to cortex in animal evolution. *Consciousness and Cognition* 14:89–114. [arBM]

Merskey, H. & Bogduk, N., eds. (1994) *Classification of chronic pain: Descriptions of chronic pain syndromes and definitions of pain terms*, pp. 209–214. IASP Press. [KJSA]

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Mesulam, M.-M. (1999) Spatial attention and neglect: Parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philosophical Transactions of the Royal Society of London, B* 354:1325–46. [aBM]

Meyer, J.-A. & Wilson, S. W., eds. (1991) *From animals to animats: Proceedings of the First International Conference on Simulation of Adaptive Behavior*. MIT Press/Bradford Books. [aBM]

Miller, E. K. & Cohen, J. D. (2001) An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience* 24:167–202. [FB]

Miller, G. A. (1986) Interview with George A. Miller. In: *The cognitive revolution in psychology*, ed. B. J. Baars, pp. 199–222. Guilford Press. [aBM, AM]

Milner, B. (1966) Amnesia following operation on the temporal lobes In: *Amnesia*, ed. C. W. M. Whitty & O. L. Zangwill, pp. 109–33. Butterworths. [EM]

Milner, P. M. (1970) *Physiological psychology*. Holt, Rinehart & Winston. [RBG]

Mitrofanis, J. (2005) Some certainty for the "zone of uncertainty"? Exploring the function of the zona incerta. *Neuroscience* 130:1–15. [arBM, TJP]

Mitrofanis, J. & Mikuletic, L. (1999) Organization of the cortical projection to the zona incerta of the thalamus. *Journal of Comparative Neurology* 412: 173–185. [aBM]

Mize, R. R., Whitworth, H., Nunes-Cardozo, B. & van der Want, J. (1994) Ultrastructural organization of GABA in the rabbit superior colliculus revealed by quantitative postembedding immunocytochemistry. *Journal of Comparative Neurology* 341:273–87. [aBM]

Montague, D. P. F. & Walker-Andrews, A. S. (2001) Peekaboo: A new look at infants' perception of emotion expressions. *Developmental Psychology* 37:826–38. [CI]

Montague, P. R., Hyman, S. E. & Cohen, J. D. (2004) Computational roles for dopamine in behavioural control. *Nature* 431:760–67. [FA]

Morcuende, S., Delgado-García, J.-M. & Ugolini, G. (2002) Neuronal premotor networks involved in eyelid responses: Retrograde transneuronal tracing with rabies virus from the orbicularis oculi muscle in the rat. *Journal of Neuroscience* 22:8808–18. [aBM]

Morin, A. (2001) The Split-Brain debate revisited: On the importance of language and self-recognition for right hemispheric consciousness. *Journal of Mind and Behavior* 22(2):107–18. [AM]

(2006) Levels of consciousness and self-awareness: A comparison and integration of various neurocognitive views. *Consciousness and Cognition* 15:358–71. [DC, CI, arBM]

Morris, D. (1967) *The naked ape: A zoologist's study of the human animal.* McGraw-Hill. [RBG]

Morris, J. S., DeGelder, B., Weiskrantz, L. & Dolan, R. J. (2001) Differential extrageniculostriate and amygdala responses to presentation of emotional faces in a cortically blind field. *Brain* 124(Pt 6):1241–52. [SW]

Morsella, E. (2005) The function of phenomenal states: Supramodular interaction theory. *Psychological Review* 112:1000–21. [EM]

Mort, E., Cairns, S., Hersch, H. & Finlay, B. (1980) The role of the superior colliculus in visually guided locomotion and visual orienting in the hamster. *Physiological Psychology* 8:20–28. [aBM]

Moruzzi, G. & Magoun, H. W. (1949) Brain stem reticular formation and activation of the EEG. *Electroencephalography and Clinical Neurophysiology* 1: 455–73. [arBM, DFW]

Moschovakis, A. K. (1996) Neural network simulations of the primate oculomotor system. II. Frames of reference. *Brain Research Bulletin* 40:337–45. [aBM]

Moschovakis, A. K. & Highstein, S. M. (1994) The anatomy and physiology of primate neurons the control rapid eye movements. *Annual Review of Neuroscience* 17:465–88. [aBM]

Mountcastle, V. B., ed. (1974) *Medical physiology*, 13th edition. C. V. Mosby. [WJF]

Mouton, L. J. (1999) *Spinal efferents and afferents of the periaqueductal gray: Possible role in pain, sex and micturition.* Doctoral dissertation, University of Groningen. [aBM]

Müller, J. R., Philiastides, M. G. & Newsome, W. T. (2004) Microstimulation of the superior colliculus focuses attention without moving the eyes. *Proceedings of the National Academy of Sciences USA* 102(3):524-29. [RJK, aBM]

Muller, U., von Cramon, D. Y. & Pollmann, S. (1998) D1- versus D2-receptor modulation of visuospatial working memory in humans. *Journal of Neuroscience* 18:2720–28. [FA]

The Multi-Society Task Force on the Persistent Vegetative State. (1994) Statement on medical aspects of the persistent vegetative state (first of two parts). *New England Journal of Medicine* 330:1499–1508. [aBM]

Mungarndee, S. S., Baldwin, B. A., Chindadoungratna C. & Kotchabhakdi, N. (2002) Hypothalamic and zona incerta neurons in sheep, initially only responding to the sight of food, also respond to the sight of water after intracerebroventricular injection of hypertonic saline or angiotensin II. *Brain Research* 925:204–12. [aBM]

Munoz, D. P. & Everling, S. (2004) Look away: The anti-saccade task and the voluntary control of eye movement. *Nature Reviews in Neuroscience* 5: 218–28. [FB]

Munoz, D. P. & Fecteau, J. H. (2002) Vying for dominance: Dynamic interactions control visual fixation and saccadic initiation in the superior colliculus. *Progress in Brain Research* 140:3–19. [RJK]

Myers, L. B. & Bulich, L. A. (2005) *Anesthesia for fetal intervention and surgery.* B. C. Decker. [RRB]

Myers, R. E. (1989) Cerebral ischemia in the developing primate fetus. *Biomedica Biochimica Acta* 48:S137–42. [aBM]

Nair, D. R., Najm, I., Bulacio, J. & Luders, H. (2001) Painful auras in focal epilepsy. *Neurology* 57:700–702. [MD]

Nandi, D., Aziz, T., Carter, H. & Stein, J. (2003) Thalamic field potentials in chronic central pain treated by periventricular gray stimulation—a series of eight cases. *Pain* 101(1-2):97–107. [KJSA]

Narsinghani, U. & Anand, K. J. S. (2000) Developmental neurobiology of pain in neonatal rats. *Lab Animal* 29(9):27–39. [KJSA]

Nashold, B. S., Wilson, W. P. & Slaughter, G. (1969) Sensations evoked by stimulation of the midbrain of man. *Journal of Neurosurgery* 30:14–24. [aBM]

Neelon, M. F., Brungart, D. S. & Simpson, B. D. (2004) The isoazimuthal perception of sounds across distance: A preliminary investigation into the location of the audio egocenter. *Journal of Neuroscience* 24:7640–47. [aBM]

Nemec, P., Altman, J., Marhold, S., Burda, H. & Oelschläger, H. H. A. (2001) Neuroanatomy of magnetoreception: The superior colliculus involved in magnetic orientation in a mammal. *Science* 294:366–68. [aBM]

Newman, J. & Baars, B. J. (1993) A neural attentional model for access to consciousness: A Global Workspace perspective. *Concepts in Neuroscience* 4(2):255–90. [DFW]

Nicolelis, M. A. L., Chapin, J. K. & Lin, R. C. (1992) Somatotopic maps within the zona incerta relay parallel GABAergic somatosensory pathways to the neocortex, superior colliculus and brainstem. *Brain Research* 577:134–41. [aBM]

Niemi-Junkola, U. J. & Westby, G. W. M. (2000) Cerebellar output exerts spatially organised influence on neural responses in the rat superior colliculus. *Neuroscience* 97:565–73. [aBM]

Nieuwenhuis, R., Ten Donkelaar, H. J. & Nicholson, C., eds. (1998) *The central nervous system of vertebrates* (4 Vols.). Springer-Verlag. [aBM]

Northcutt, R. G. (1996a) The Agnathan ark: The origin of the craniate brain. *Brain, Behavior and Evolution* 48:237–47. [aBM]

(1996b) The origin of craniates: neural crest, neurogenic placodes, and homeobox genes. *Israel Journal of Zoology* 42:S273–13. [aBM]

Northcutt, R. G. & Wicht, H. (1997) Afferent and efferent connections of the lateral and medial pallia of the silver lamprey. *Brain, Behavior and Evolution* 49: 1–19. [aBM]

Northoff, G. & Bermpohl, F. (2004) Cortical midline structures and the self. *Trends in Cognitive Science* 8(3):102–107. [GN]

Northoff, G., Heinzel, A., de Greck, M., Bermpohl, F., Dobrowolny, H. & Panksepp, J. (2006) Self-referential processing in our brain: A meta-analysis of imaging studies on the self. *Neuroimage* 31(1): 440–57. [aBM, GN]

Nudo, R. J. & Masterton, R. B. (1988) Descending pathways to the spinal cord: A comparative study of 22 mammals. *Journal of Comparative Neurology* 277: 53–79. [aBM]

Oakley, D. A. (1983) The varieties of memory: A phylogenetic approach. In: *Memory in animals and humans*, ed. A. Mayes, pp. 20–82. Van Nostrand Reinhold. [aBM]

Oakley, T. H. & Cunningham, C. W. (2002) Molecular phylogenetic evidence for the independent evolutionary origin of the arthropod compound eye. *Proceedings of the National Academy of Sciences USA* 99:1426. [DBE]

Ohman, A. (2005) The role of the amygdala in human fear: Automatic detection of threat. *Psychoneuroendocrinology* 30:953–58. [CI]

O'Keefe, J. & Nadel, L. (1978) *The hippocampus as a cognitive map*. Clarendon Press. [WJF]

O'Leary, D. D., Schlaggar, B. L. & Stanfield, B. B. (1992) The specification of sensory cortex: Lessons from cortical transplantation. *Experimental Neurology* 115(1):121–26. [KJSA]

Olson, E. J., Boeve, B. F. & Silber, M. H. (2000) Rapid eye movement sleep behaviour disorder: Demographic, clinical and laboratory findings in 93 cases. *Brain* 123:331–39. [DC]

Onofrj, M., Bonanni, L., Albani, G., Mauro, A., Bulla, D. & Thomas, A. (2006) Visual hallucinations in Parkinson's disease: Clues to separate origins *Journal of the Neurological Sciences* 248:143–50. [DC]

O'Regan, J. K., Deubel, H., Clark, J. J. & Rensink, R. A. (2000) Picture changes during blinks: Looking without seeing and seeing without looking. *Visual Cognition* 7:191–211. [aBM]

Orlovsky, G. N. & Shik, M. L. (1976) Control of locomotion: A neurophysiological analysis of the cat locomotor system. *International Review of Physiology* 10:281–317. [aBM]

O'Shea, R. P. & Corballis, P. M. (2005) Visual grouping on binocular rivalry in a split-brain observer. *Vision Research* 45:247–61. [EM]

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Owen, A. M., Coleman, M. R., Boly, M., Davis, M. H., Laureys, S. & Pickard, J. D. (2006) Detecting awareness in the vegetative state. *Science* 313(5792):1402. [SW]

Özen, G., Augustine, G. J. & Hall, W. C. (2000) Contribution of superficial layer neurons to premotor bursts in the superior colliculus. *Journal of Neurophysiology* 84:460–71. [arBM]

Padel, Y. (1993) Magnocellular and parvocellular red nuclei. Anatomico-functional aspects and relations with the cerebellum and other nerve centres. [Article in French]. *Revue Neurologique (Paris)* 149:703–15. [aBM]

Palmer, L. A., Rosenquist, A. C. & Sprague, J. M. (1972) Corticotectal systems in the cat: Their structure and function. In: *Corticothalamic projections and sensorimotor activities*, ed. T. Frigyesi, E. Rinvik & M. D. Yahr, pp. 491–522. Raven Press. [aBM]

Panksepp, J. (1982) Toward a general psychobiological theory of emotions. *Behavioral and Brain Sciences* 5:407–67. [aBM]

(1998a) *Affective neuroscience: The foundations of human and animal emotions.* Oxford University Press. [CI, aBM, GN, JP, DFW]

(1998b) The periconscious substrates of consciousness: Affective states and the evolutionary origins of the self. *Journal of Consciousness Studies* 5(5–6): 566–82. [GN, JP]

(2003) At the interface of the affective, behavioral, and cognitive neurosciences: Decoding the emotional feelings of the brain. *Brain and Cognition* 52(1): 4–14. [GN]

(2005a) Affective consciousness: Core emotional feelings in animals and humans. *Consciousness and Cognition* 14(1):30–80. [GN, JP, JvH]

(2005b) On the embodied neural nature of core emotional affects. *Journal of Consciousness Studies* 12:158–84. [CI]

(2006) Emotional endophenotypes in evolutionary psychiatry. *Progress in Neuro-Psychopharmacology and Biological Psychiatry* 30:774–84. [JP]

Panksepp, J. & Burgdorf, J. (1999) Laughing rats? Playful tickling arouses high frequency ultrasonic chirping in young rodents. In: *Toward a science of consciousness, vol. III*, ed. S. Hameroff, D. Chalmers & A. Kazniak, pp. 231–44. MIT Press. [JP]

(2003) "Laughing" rats and the evolutionary antecedents of human joy? *Physiology and Behavior* 79:533–47. [JP]

Panksepp, J., Normansell, L., Cox, J. F. & Siviy, S. M. (1994) Effects of neonatal decortication on the social play of juvenile rats. *Physiology and Behavior* 56:429–43. [aBM, JP]

Panksepp, J. & Panksepp, J. B. (2000) The sevens sins of evolutionary psychology. *Evolution and Cognition* 6:108–31. [JvH]

Parmelee, P. A. (1996) Pain in cognitively impaired older persons. *Clinics in Geriatric Medicine* 12(3):473–87. [KJSA]

Parvizi, J. & Damasio, A. R. (2001) Consciousness and the brainstem. *Cognition* 79:135–60. [aBM]

(2003) Neuroanatomical correlates of brainstem coma. *Brain* 126:1524–36. [aBM]

Pellis, S. M., Pellis, V. C. & Whishaw, I. Q. (1992) The role of the cortex in play fighting by rats: Developmental and evolutionary implications. *Brain, Behavior and Evolution* 39:270–84. [aBM]

Penfield, W. (1952) Epileptic automatisms and the centrencephalic integrating system. *Research Publications of the Association for Nervous and Mental Disease* 30:513–28. [FA, aBM]

Penfield, W. & Jasper, H. H. (1954) *Epilepsy and the functional anatomy of the human brain*. Little, Brown. [KJSA, R-PB, RRB, AMLC, DBE, WJF, RBG, arBM]

Penfield, W. & Rasmussen, T. (1955) *The cerebral cortex of man*. MacMillan. [MD]

Pereira, L. C., Modesto, A. M., Sugai, R. & daMota, L. A. (2005) Pain sensitive cerebral areas and intracranial structures revealed at fully awake craniotomies for primary intracranial tumor resection. *Abstracts IASP 11th World Congress on Pain*, 1517:P20. IASP Press. [MD]

Pernick, M. S. (1985) "They don't feel it like we do": Social politics and the perception of pain. In: *A calculus of suffering: Pain, professionalism, and anesthesia in nineteenth-century America*, by M. S. Pernick, pp. 148–70. Columbia University Press. [KJSA]

Perry, D. C. & Kellar, K. J. (1995) [3H]epibatidine labels nicotinic receptors in rat brain: An autoradiographic study. *Journal of Pharmacology and Experimental Therapeutics* 275:1030–34. [DC]

Perry, E. K., Court, J. A., Johnson, M., Smith, C. J., James, V., Cheng, A. V., Kerwin, J. M., Morris, C. M., Piggott, M. A., Edwardson, J. A., Birdsall, N. J. M., Turner, J. T. & Perry, R. H. (1993) Autoradiographic comparison of cholinergic and other transmitter receptors in the normal human hippocampus. *Hippocampus* 3:307–15. [DC]

Perry, E. K., Irving, D., Kerwin, J. M., McKeith, I. G., Thompson, P., Collerton, D., Fairbairn, A. F., Ince, P. G., Morris, C. M., Cheng, A. V. & Perry, R. H. (1993) Cholinergic transmitter and neurotrophic activities in Lewy body dementia: Similarity to Parkinson's and distinction from Alzheimer disease. *Alzheimer Disease and Associated Disorders* 7:69–79. [DC]

Perry, E. K., Morris, C. M., Court, J. A., Cheng, A., Fairbairn, A. F., McKeith, I. G., Irving, D., Brown, A. & Perry, R. H. (1995) Alteration in nicotine binding sites in Parkinson's disease, Lewy body dementia and Alzheimer's disease: Possible index of early neuropathology. *Neuroscience* 64:385–95. [DC]

Perry, E. K. & Piggott, M. A. (2000) Neurotransmitter mechanisms of dreaming: Implications of modulatory systems abased on dream intensity. *Behavioral and Brain Sciences* 23:990–92. [DC]

Perry, E. K., Walker, M., Grace, J. & Perry, R. (1999) Acetylcholine in mind: A neurotransmitter correlate of consciousness? *Trends in the Neurosciences*. 22:273–80. [DC]

Persaud, N., McLeod, P. & Cowey, A. (2007) Post-decision wagering objectively measures awareness. *Nature Neuroscience* 10:257–61. [rBM]

Petrides, M. & Pandya, D. N. (2002) Association pathways of the prefrontal cortex and functional observations. In: *Principles of frontal lobe function*, ed. D. T. Stuss & R. T. Knight, pp. 31–50. Oxford University Press. [FB]

Petty, P. G. (1998) Consciousness: A neurosurgical perspective. *Journal of Consciousness Studies* 5:86–96. [aBM]

Peyron, R., Laurent, B. & Garcia-Larrea, L. (2000) Functional imaging of brain responses to pain: A review and meta-analysis. *Neurophysiologie Clinique* 30:263–88. [MD]

Phan, K. L., Taylor, S. F., Welsh, R. C., Ho, S. H., Britton, J. C. & Liberzon, I. (2004) Neural correlates of individual ratings of emotional salience: A trial-related fMRI study. *Neuroimage* 21(2): 768–80. [GN]

Philipona, D., O'Reagan, J. K. & Nadal, J.-P. (2003) Is there something out there? Inferring space from sensorimotor dependencies. *Neural Computation* 15:2029–49. [aBM]

Philipona, D., O Regan, J. K., Nadal, J.-P. & Coenen, O. J.-M. D. (2004) Perception of the structure of the physical world using multimodal unknown sensors and effectors. *Advances in Neural Information Processing Systems* 16: 945–52. [aBM]

Phillips, P. E., Stuber, G. D., Heien, M. L., Wightman, R. M. & Carelli, R. M. (2003) Subsecond dopamine release promotes cocaine seeking. *Nature* 422:614–18. [FA]

Pierrot-Deseilligny, C., Rivaud, S., Gaymard, B. & Agid, Y. (1991) Cortical control of reflexive visually-guided saccades. *Brain* 114:1473–85. [FB]

Pimlott, S. L., Piggott, M., Ballard, C., McKeith, I., Perry, R., Kometa, S., Owens, J., Wyper, D. & Perry, E. (2006) Thalamic nicotinic receptors implicated in disturbed consciousness in dementia with Lewy bodies. *Neurobiology of Disease*. 21:50–56. [DC]

Plotnik, J. M., de Waal, F. B. M. & Reiss, D. (2006) Self-recognition in an Asian elephant. *Proceedings of the National Academy of Sciences USA* 103: 17053–17057. [EG]

Pockett, S. (2006) The great subjective back-referral debate: Do neural responses increase during a train of stimuli? *Consciousness and Cognition* 15:551–59. [rBM]

Pollen, D. A. (2003) Explicit neural representations, recursive neural networks and conscious visual perception. *Cerebral Cortex* 13:807–14. [rBM]

Pombal, M. A., El Manira, A. & Grillner, S. (1997) Afferents of the lamprey striatum with special reference to the dopaminergic system: A combined tracing and immunohistochemical study. *Journal of Comparative Neurology* 386:71–91. [rBM]

Pöppel, E. & Richards, W. (1974) Light sensitivity in cortical scotomata contralateral to small islands of blindness. *Experimental Brain Research* 21:125–30. [rBM]

Populin, L. C. & Yin, T .C. T. (1998) Sensitivity of auditory cells in the superior colliculus to eye position in the behaving cat. In: *Psychological and physiological advances in hearing*, ed. A. R. Palmer, A. Q. Summerfield & R. Meddis, pp 441–48. Whurr. [aBM]

Porges, S. W. (2001) The polyvagal theory: Phylogenetic substrates of a social nervous system. *International Journal of Psychophysiology* 42123–46. [JvH]

Porter, F. L. & Anand, K. J. S. (1998) Epidemiology of pain in neonates. *Research & Clinical Forums* 20(4):9–16. [KJSA]

Posner, M. I. & Petersen, S. E. (1990) The attention systems of the human brain. *Annual Review of Neuroscience* 13:25–42. [FB, aBM]

Posner, M. I. & Rothbart, M. (2000) Developing mechanisms of self-regulation. *Development and Psychopathology* 12:427–41. [CI]

Povinelli, D. J. (1989) Failure to find self-recognition in Asian elephants (*Elephas maximus*) in contrast to their use of mirrors cues to discover hidden food. *Journal of Comparative Psychology* 102:122–31. [EG]

Power, B. D., Kolmac, C. I. & Mitrofanis, J. (1999) Evidence for a large projection from the zona incerta to the dorsal thalamus. *Journal of Comparative Neurology* 404:554–65. [aBM]

Power, B. D. & Mitrofanis, J. (1999) Evidence for extensive inter-connections within the zona incerta in rats. *Neuroscience Letters* 267:9–12. [aBM]

(2001) Zona incerta: Substrate for the contralateral interconnectivity in the thalamus of rats. *Journal of Comparative Neurology* 436:52–63. [aBM]

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Prescott, T. J., Redgrave, P. & Gurney, K. N. (1999) Layered control architectures in robots and vertebrates. *Adaptive Behavior* 7(1):99–127. [arBM, TJP, AKS]
Provine, R. R. & Yong, Y. L. (1991) Laughter: A stereotyped human vocalization. *Ethology* 89:115–24. [aBM]
Quinn, P. C., Slater, A. M., Brown, E. & Hayes, R. A. (2001). Developmental change in form categorization in early infancy. *British Journal of Developmental Psychology* 19:207–18. [CI]
Rada, E. M., Tharakan, E. C. & Flood, P. (2003) Volatile anesthetics reduce agonist affinity at nicotinic acetylcholine receptors in the brain. *Anesthesia and Analgesia* 96:108–11. [DC]
Rainville, P., Duncan, G. H., Price, D. D., Carrier, B. & Bushnell, M. C. (1997) Pain affect encoded in human anterior cingulate but not somatosensory cortex. *Science* 277:968–71. [MD]
Ramón-Moliner, E. & Nauta, W. J. H. (1966) The isodendritic core of the brainstem. *Journal of Comparative Neurology* 126:311–35. [aBM]
Rankin, C. H. (2002) From gene to identified neuron to behaviour in *Caenorhabditis elegans*. *Nature Reviews Genetics* 3:622–30. [SMD]
Ray, M., Bohr, I., McIntosh, J. M., Ballard, C., McKeith, I., Chalon, S., Guilloteau, D., Perry, R., Perry, E., Court, J. A. & Piggott, M. (2004) Involvement of alpha6/alpha3 neuronal nicotinic acetylcholine receptors in neuropsychiatric features of Dementia with Lewy bodies: [(125)I]-alpha-conotoxin MII binding in the thalamus and striatum. *Neuroscience Letters* 372:220–25. [DC]
Raz, A. & Buhle, J. (2006) Typologies of attentional networks. *Nature Reviews Neuroscience* 7:367–79. [aBM]
Reddy, L., Reddy, L. & Koch, C. (2006) Face identification in the near-absence of focal attention. *Vision Research* 46:2336–2343. [rBM]
Redgrave, P. & Gurney, K. (2006) The short-latency dopamine signal: A role in discovering novel actions? *Nature Reviews Neuroscience* 7:967–75. [FA]
Redgrave P., McHaffie, J. G. & Stein, B. E. (1996a) Nociceptive neurons in rat superior colliculus I: Antidromic activation from the contralateral predorsal bundle. *Experimental Brain Research* 109:185–96. [rBM]
Redgrave, P., Prescott, T. & Gurney, K. N. (1999) The basal ganglia: A vertebrate solution to the selection problem? *Neuroscience* 89:1009–23. [TJP]
Redgrave, P., Simkins, M., McHaffie, J. G. & Stein, B. E. (1996b) Nociceptive neurons in rat superior colliculus II: Effects of lesions to contralateral descending output pathway on nocifensive behaviors. *Experimental Brain Research* 109:197–208. [rBM]
Rees, G. (2001) Neuroimaging of visual awareness in patients and normal subjects. *Current Opinion in Neurobiology* 11:150–56. [aBM]
Rees, G., Kreiman, G. & Koch, C. (2002) Neural correlates of consciousness in humans. *Nature Reviews Neuroscience* 3(4):261–70. [SMD, SW]
Rees, G. & Lavie, N. (2001) What can functional imaging reveal about the role of attention in visual awareness? *Neuropsychologia* 39:1343–53. [aBM]
Reiner, A., Yamamoto, K. & Karten, H. J. (2005) Organization and evolution of the avian forebrain. *Anatomical Record Part A, Discoveries in Molecular, Cellular, and Evolutionary Biology* 287(1):1080–102. [DBE]
Reiss, D. & Marino, L. (2001) Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proceedings of the National Academy of Sciences USA* 98:5937–42. [EG]
Rensink, R.A. (2002) Change detection. *Annual Review of Psychology* 53: 245–77. [aBM]
Rensink, R.A., O'Regan, J. K. and Clark, J. J. (1997) To see or not to see: The need for attention to perceive changes in scenes. *Psychological Science* 8: 368–73. [aBM]
Ressler, N. (2004) Rewards and punishments, goal-directed behavior and consciousness. *Neuroscience and Biobehavioral Reviews* 28:27–39. [JvH]
Richards, W., Seung H. S. & Pickard, G. (2006) Neural voting machines. *Neural Networks* 19:1161-67. [aBM]
Rieck, R. W., Huerta, M. F., Harting, J. K. & Weber, J. T. (1986) Hypothalamic and ventral thalamic projections to the superior colliculus in the cat. *Journal of Comparative Neurology* 243:249–65. [aBM]
Rock, I. (1995) *Perception*. Scientific American Library/W. H. Freeman. [RBG]
Roelofs, C. O. (1959) Considerations on the visual egocenter. *Acta Psychologica* 16:226–34. [aBM]
Rolls, E. T. (1999) *The brain and emotion*. Oxford University Press. [JvH]
Rosenthal, D. M. (2002) How many kinds of consciousness? *Consciousness and Cognition* 11:653–65. [CI]
Rossetti, Z. L. & Carboni, S. (2005) Noradrenaline and dopamine elevations in the rat prefrontal cortex in spatial working memory. *Journal of Neuroscience* 25(9):2322–29. [FA]
Roth, G. (1987) *Visual behavior in salamanders*. Springer-Verlag. [WJF]
Royal College of Obstetricians and Gynecologists (1997) *Fetal Awareness: Report of a Working Party*. RCOG Press. [RRB]
Rushmore, R. J., Valero-Cabre A., Lomber, S. G., Hilgetag, C. C. & Payne, B. R. (2006) Functional circuitry underlying visual neglect. *Brain* 29:1803–21. [rBM]
Sachs, E. (1967) Dissociation of learning in rats and its similarities to dissociative states in man. In: *Comparative psychopathology: Animal and human*, ed. J. Zubin & H. Hunt, pp. 249–304. Grune & Stratton. [rBM]
Sahraie, A., Weiskrantz, L., Barbur, J. L., Simmons, A., Williams, S. C. & Brammer, M. J. (1997) Pattern of neuronal activity associated with conscious and unconscious processing of visual signals. *Proceedings of the National Academy of Sciences USA* 94(17):9406–11. [SW]
Sakuma, Y. & Pfaff, D. W. (1979) Facilitation of female reproductive behavior from mesencephalic central gray in the rat. *American Journal of Physiology* 237:R278–84. [aBM]
Satterlie, R. A. & Nolen, T. G. (2001) Why do cubomedusae have only four swim pacemakers? *Journal of Experimental Biology* 204:1413–19. [aBM]
Schaefer, K. P. & Schneider, H. (1968) Reizversuche im tectum opticum des Kaninchens. Ein experimenteller Beitrag zur sensorimotorischen Koordination des Hirnstammes. *Archiv für Psychiatrie und Nervenkrankheiten* 211:118–37. [aBM]
Schall, J. D. (1997) Visuomotor areas of the frontal lobe. *Cerebral Cortex* 12: 527–638. [aBM]
Schaller, G. B. (1972) *The Serengeti lion*. University of ChicagoPress. [EG]
Scheibel, M. E. & Scheibel, A. B. (1967) Anatomical basis of attention mechanisms in vertebrate brains. In: *The neurosciences, a study program*, ed. G. C. Quarton, T. Melnechuk & F. O. Schmitt, pp. 577–602. Rockefeller University Press. [TJP]
(1977) The anatomy of constancy. *Annals of the New York Academy of Sciences* 290:421–35. [aBM]
Schiller, P. H. & Koerner, F. (1971) Discharge characteristics of single units in superior colliculus of the alert Rhesus monkey. *Journal of Neurophysiology* 43:920–36. [aBM]
Schiller, P. H. & Lee, K. (1994) The effects of lateral geniculate nucleus, area V4, and middle temporal (MT) lesions on visually guided eye movements. *Visual Neuroscience* 11:229–41. [aBM]
Schiller, P. H., True, S. D. & Conway, J. L. (1979) Effects of frontal eye field and superior colliculus ablations on eye movements. *Science* 206:590–92. [aBM]
Schlag-Rey, M., Schlag, J. & Dassonville, P. (1992) How the frontal eye fields impose a saccade goal on superior colliculus neurons. *Journal of Neurophysiology* 67:1003–1005. [aBM]
Schmidtke, K. & Buttner-Ennever, J. A. (1992) Nervous control of eyelid function. A review of clinical, experimental and pathological data. *Brain* 115:227–47. [aBM]
Schneider, F., Rotte, M., Dahlem, Y. Bogerts, B., Tempelmann, C., Heinze, H. J Walter, M. & Northoff, G. (submitted) Modulation of the resting state in cortical midline structures by self-relatedness. [GN]
Schneider, G. E. (1967) Contrasting visuomotor functions of tectum and cortex in the golden hamster. *Psychologische Forschung* 31:52–62. [aBM]
Schneider, K. A. & Kastner, S. (2005) Visual responses of the human superior colliculus: A high-resolution functional magnetic resonance imaging study. *Journal of Neurophysiology* 94(4):2491–03. [SW]
Schneider, W. X. & Deubel, H. (2002) Selection-for-perception and selection-for-spatial-motor-action are coupled by visual attention: A review of recent findings and new evidence from stimulus-driven saccade control. In: *Attention and performance XIX: Common mechanisms in perception and action*, ed. W. Prinz & B. Hommel, pp. 609–27. Oxford University Press. [aBM]
Schooler, J. W. (2002) Re-representing consciousness: Dissociations between experience and meta-consciousness. *Trends in Cognitive Sciences* 6(8): 339–44. [AM]
Schopenhauer, A. (1819/1958) *The world as will and representation* (2 vols.), trans. E. F. J. Payne. Dover. [aBM, R-PB]
Schuller, G. & Radtke-Schuller, S. (1990) Neural control of vocalization in bats: Mapping of brainstem areas with electrical microstimulation eliciting species-specific echolocation calls in the rufous horseshoe bat. *Experimental Brain Research* 79:192–206. [aBM]
Schultz, W. & Dickinson, A. (2000) Neuronal coding of prediction errors. *Annual Review of Neuroscience* 23:473–500. [FA]
Schutter, D. J. L. G. & Van Honk, J. (2004a) Extending the global workspace theory to emotion: Phenomenality without access. *Consciousness and Cognition* 13:539–49. [JvH]
(2004b) Schizophrenia: A disorder of affective consciousness. *Behavioral and Brain Sciences* 27:804–805. [JvH]
Schwartz, B. L. (2005) Do nonhuman primates have episodic memory? In: *The missing link in cognition: Origins of self-reflective consciousness*, ed. H. S. Terrace & J. Metcalfe, pp. 225–41. Oxford University Press. [AM]
Searle, J. R. (1983) *Intentionality: An essay on the philosophy of mind*. Cambridge University Press. [JP]
(1992) *The rediscovery of the mind*. MIT Press/Bradford Books. [R-PB, aBM]
(1997) *The mystery of consciousness*. Granta. [R-PB]
Seth, A. K. (2005) Causal connectivity analysis of evolved neural networks during behavior. *Network: Computation in Neural Systems* 16(1):35–55. [AKS]
(in press) The ecology of action selection: Insights from artificial life. *Philosophical Transactions of the Royal Society of London, B: Biological Sciences*. [AKS]

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

Seth, A. K., Baars, B. J. & Edelman, D. B. (2005) Criteria for consciousness in humans and other mammals. *Consciousness and Cognition* 14(1):119–39. [DBE, rBM, AKS]

Seth, A. K., Izhikevich, E., Reeke, G. N. & Edelman, G. M. (2006) Theories and measures of consciousness: An extended framework. *Proceedings of the National Academy of Sciences USA* 103(28):10799–804. [AKS]

Sewards, T. V. & Sewards, M. A. (2000) Visual awareness due to neuronal activities in subcortical structures: A proposal. *Consciousness and Cognition* 9: 86–116. [arBM]

Shapiro, B. S. (1999) Implications for our definitions of pain. *Pain Forum* 8: 100–102. [KJSA]

Shapiro, L. A. (2004) *The mind incarnate*. MIT Press. [GP]

Sharp, P. E., Blair, H. T. & Cho, J. (2001) The anatomical and computational basis of the rat head-direction cell signal. *Trends in Neurosciences* 24:289–94. [rBM]

Shepherd, G. M. & Greer, C. A. (1998) Olfactory bulb. In: *The synaptic organization of the brain*, 4th edition, ed. G. M. Shepherd, pp. 159–204. Oxford University Press. [EM]

Shergill, S. S., Brammer, M. J., Williams, S. C., Murray, R. M. & McGuire, P. K. (2000) Mapping auditory hallucinations in schizophrenia using functional magnetic resonance imaging. *Archives of General Psychiatry* 57: 1033–38. [R-PB]

Sherman, H. B., Caviness, V.S., Jr. & Ingle, D. J. (1979) Corticotectal connections in the gerbil. *Neuroscience Abstract* 9:120. [aBM]

Sherman, S. M. (1974) Visual fields of cats with cortical and tectal lesions. *Science* 185:355–57. [aBM]

(1977) The effect of superior colliculus lesions upon the visual fields of cats with cortical ablations. *Journal of Comparative Neurology* 172:211–30. [aBM]

Sherman, S. M. & Guillery, R. W. (2001) *Exploring the thalamus.* Academic Press. [aBM]

Shewmon, D. A. (2004) The ABC of PVS. In: *Brain death and disorders of consciousness*, ed. C. Machado & D. A. Shewmon, pp. 215–28. Kluwer Academic/ Plenum. [aBM]

Shewmon, D. A., Capron, A. M., Peacock, W. J. & Shulman, B. L. (1989) The use of anencephalic infants as organ sources. A critique. *Journal of the American Medical Association* 261:1773–81. [aBM]

Shewmon, D. A., Holmes, G. L. & Byrne, P. A. (1999) Consciousness in congenitally decorticate children: Developmental vegetative state as self-fulfilling prophecy. *Developmental Medicine and Child Neurology* 41:364–74. [DBE, aBM, JP]

Shieber, S. M., ed. (2004) *The Turing test: Verbal behavior as the hallmark of intelligence*. MIT Press. [RBG]

Shiller, V. M., Izard, C. E. & Hembree, E. A. (1986) Patterns of emotion expression during separation in the Strange Situation procedure. *Developmental Psychology* 22:378–82. [CI]

Silvia, P. J. (2006) *Exploring the psychology of interest*. Oxford University Press. [CI]

Simons, D. J. & Chabris, C. F. (1999) Gorillas in our midst: Sustained inattentional blindness for dynamic events. *Perception* 28:1059–74. [aBM]

Simons, S. H. P., van Dijk, M., Anand, K. J. S., Roofthooft, D., van Lingen, R. A. & Tibboel, D. (2003) Do we still hurt newborn babies? A prospective study of procedural pain and analgesia in neonates. *Archives of Pediatrics and Adolescent Medicine* 157:1058–64. [KJSA]

Singer, W. (2001) Consciousness and the binding problem. In: *Cajal and consciousness: Scientific approaches to consciousness on the centennial of Ramón y Cajal's Textura*, ed. P. C. Marijuán. *Annals of the New York Academy of Science* 929:123–46. [aBM]

Slater, R., Cantarella, A., Gallella, S., Worley, A., Boyd, S., Meek, J. & Fitzgerald, M. (2006) Cortical pain responses in human infants. *Journal of Neuroscience* 26(14):3662–66. [KJSA]

Smeets, W. J. A. J., Marín, O. & Gonzáles, A. (2000) Evolution of the basal ganglia: New perspectives through a comparative approach. *Journal of Anatomy* 196:501–17. [rBM]

Smith, S. (1996) *Commission of inquiry into fetal sentience*. CARE. [RRB]

Snaith, S. & Holland, O. (1990) An investigation of two mediation strategies suitable for behavioural control in animals and animats. In: *From animals to animats: Proceedings of the First International Conference on Simulation of Adaptive Behavior*, ed. J.-A. Meyer & S. Wilson, pp. 255–62. MIT Press. [aBM]

Snodgrass, R. E. (1935) *Principles of insect morphology.* McGraw-Hill. [aBM]

Sokolov, E. N. (1963) *Perception and the conditioned reflex.* Pergamon Press. [FB]

Sommer, M. A. & Wurtz, R. H. (2004) What the brain stem tells the frontal cortex. I. Oculomotor signals sent from superior colliculus to frontal eye field via mediodorsal thalamus. *Journal of Neurophysiology* 91:1381–402. [aBM]

Sparks, D. L. (1999) Conceptual issues related to the role of the superior colliculus in the control of gaze. *Current Opinion in Neurobiology* 9:698–707. [aBM]

Sparks, D. L. & Jay, M. F. (1986) The functional organization of the primate superior colliculus: A motor perspective. *Progress in Brain Research* 64: 235–241. [FA]

Sperry, R. W. (1952) Neurology and the mind-brain problem. *American Scientis*, 40:291–312. [EM]

Sporns, O., Tononi, G. & Edelman, G. M. (2000) Theoretical neuroanatomy: Relating anatomical and functional connectivity in graphs and cortical connection matrices. *Cerebral Cortex* 10:127–41. [aBM, AKS]

Sprague, J. M. (1966) Interaction of cortex and superior colliculus in mediation of visually guided behavior in the cat. *Science* 153:1544–47. [aBM]

(1975) Mammalian tectum: Intrinsic organization, afferent inputs, and integrative mechanisms. In: *Sensorimotor function of the midbrain tectum*, ed. D. Ingle & J. M. Sprague. *Neurosciences Research Program Bulletin* 13:204–14. MIT Press. [aBM]

(1991) The role of the superior colliculus in facilitating visual attention and form perception. *Proceedings of the National Academy of Sciences USA* 88: 1286–90. [aBM]

(1996) Neural mechanisms of the visual orienting response. *Progress in Brain Research* 112:1–15. [aBM, SW]

Sprague, J. M., Chambers, W. W. & Stellar, E. (1961) Attentive, affective, and adaptive behavior in the cat. *Science* 133:165–73. [aBM]

Spurden, D. P., Court, J. A., Lloyd, S., Oakley, A., Perry, R., Pearson, C., Pullen, R. G. & Perry, E. K. (1997) Nicotinic receptor distribution in the human thalamus: Autoradiographical localization of [3H]nicotine and [125I] alpha-bungarotoxin binding. *Journal of Chemical Neuroanatomy* 13:105–13. [DC]

Stallard, P., Williams, L., Lenton, S. & Velleman, R. (2001) Pain in cognitively impaired, non-communicating children. *Archives of Disease in Childhood* 85(6):460–462. [KJSA]

Standing, L. (1973) Learning 10,000 pictures. *Quarterly Journal of Experimental Psychology* 25:207–22. [aBM]

Steele, G. E. & Weller, R. E. (1993) Subcortical connections of subdivisions of inferior temporal cortex in squirrel monkeys. *Visual Neuroscience* 10: 563–83. [aBM]

Stefan, H. & Snead, O. C. (1997) Absence seizures. In *Epilepsy: A comprehensive textbook*, ed. J. Engel, Jr. & T. A. Pedley, pp. 579–90. Lippincott-Raven. [aBM]

Steriade, M. (2001) Impact of network activities on neuronal properties in corticothalamic systems. *Journal of Neurophysiology* 86:1–39. [aBM]

Steriade, M., Jones, E. & Llinas, R. (1990) *Thalamic oscillations and signaling.* Wiley. [SMD]

Stoerig, P. & Barth, E. (2001) Low-level phenomenal vision despite unilateral destruction of primary visual cortex. *Consciousness and Cognition* 10: 574–87. [arBM]

Strafstrom, C. E. (2006) Epilepsy: A review of selected clinical syndromes and advances in basic science. *Journal of Cerebral Blood Flow and Metabolism* 26:983–1004. [aBM]

Strigo, I. A., Duncan, G. H., Boivin, M. & Bushnell, M. C. (2003) Differentiation of visceral and cutaneous pain in the human brain. *Journal of Neurophysiology* 89:3294–303. [MD]

Stuphorn, V., Bauswein, E. & Hoffmann, K.-P. (2000) Neurons in the primate superior colliculus coding for arm movements in gaze-related coordinates. *Journal of Neurophysiology* 83:1283–99. [aBM]

Sumner, P., Tsai, P. C., Yu, K. & Nachev, P. (2006) Attentional modulation of sensorimotor processes in the absence of perceptual awareness. *Proceedings of the National Academy of Sciences USA* 103(27):10520–25. [SW]

Sutton, L. N., Bruce, D. A. & Schut, L. (1980) Hydranencephaly versus maximal hydrocephalus: An important clinical distinction. *Neurosurgery* 6: 34–38. [aBM]

Swanson, L. W. (1987) The hypothalamus. In: *Handbook of chemical neuroanatomy. Integrated systems of the CNS, Part 1, vol. 5*, ed. T. Hökfelt, A. Björklund & L. W. Swanson, pp. 1–124. Elsevier. [aBM]

(2000) Cerebral hemisphere regulation of motivated behavior. *Brain Research* 886:113–64. [arBM]

Sylvester, R., Driver, J. & Rees, G. (2007) Visual fMRI responses in human superior colliculus show a temporal-nasal asymmetry that is absent in lateral geniculate and visual cortex. *Journal of Neurophysiology* 86:1495–502. [SW]

Takada, K., Shiota, M., Ando, M., Kimura, M. & Inoue, K. (1989) Porencephaly and hydranencephaly: a neuropathological study of four autopsy cases. *Brain and Development* 11:51–56. [aBM]

Tarsitano, M. S. & Andrew, R. (1999) Scanning and route selection in the jumping spider *Portia labiata. Animal Behaviour* 58:255–65. [EG]

Tehovnik, E .J., Lee, K. & Schiller, P. H. (1994) Stimulation-evoked saccades from the dorsomedial frontal cortex of the rhesus monkey following lesions of the frontal eye fields and superior colliculus. *Experimental Brain Research* 98:179–90. [aBM]

Telford, S., Wang, S. & Redgrave, P. (1996) Analysis of nociceptive neurones in the rat superior colliculus using c-fos immunohistochemistry. *Journal of Comparative Neurology* 375:601–17. [rBM]

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

ten Donkelaar, H. J. (1988) Evolution of the red nucleus and rubrospinal tract. *Behavioral Brain Research* 28:920. [aBM]
Termine, N. T. & Izard, C. E. (1988) Infants' responses to their mothers' expressions of joy and sadness. *Developmental Psychology* 24:223–29. [CI]
Terrace, H. S. & Metcalfe, J., eds. (2005) *The missing link in cognition: Origins of self-reflective consciousness*. Oxford University Press. [AM]
Thompson, R. (1993) Centrencephalic theory, the general learning system, and subcortical dementia. *Annals of the New York Academy of Sciences* 702: 197–223. [FA, aBM, TJP]
Thompson, R & Bachman, M. K. (1979) Zona incerta: A link between the visual cortical sensory system and the brainstem motor system. *Physiological Psychology* 7:251–53. [aBM]
Tinbergen, N. (1951) *The study of instinct*. Clarendon Press. [aBM]
Tiraboschi, P., Hansen, L. A., Alford, M., Merdes, A., Masliah, E., Thal, L. J. & Corey-Bloom, J. (2002) Early and widespread cholinergic losses differentiate dementia with Lewy bodies from Alzheimer disease. *Archives of General Psychiatry* 59:946–51. [DC]
Tobler, P. N., Dickinson, A. & Schultz, W. (2003) Coding of predicted reward omission by dopamine neurons in a conditioned inhibition paradigm. *Journal of Neuroscience* 23:10402–10. [FA]
Todd, P. M. & Gigerenzer, G. (2000). Précis of *Simple heuristics that make us smart*. *Behavioral and Brain Sciences* 23727–81. [RAG]
Tong, F. (2003) Primary visual cortex and visual awareness. *Nature Reviews Neuroscience* 4:210–20. [rBM]
Tononi, G. (2004) An information integration theory of consciousness. *BMC Neuroscience* 5(1):42. [SMD, AKS]
Tononi, G. & Edelman, G. M. (1998) Consciousness and complexity. *Science* 282(5395):1846–51. [SMD, AKS]
Trageser, J. C., Burke, K. A., Masri, R., Li, Y., Sellers, L. & Keller, A. (2006) State-dependent gating of sensory inputs by zona incerta. *Journal of Neurophysiology* 96:1456–63. [TJP]
Trageser, J. C. & Keller, A. (2004) Reducing the uncertainty: Gating of peripheral inputs by zona incerta. *Journal of Neuroscience* 24:8911–9005. [aBM]
Tresch, D. D., Farrol, H. S., Duthie, E. H., Goldstein, M. D. & Lane, P. S. (1991) Clinical characteristics of patients in the persistent vegetative state. *Archives of Internal Medicine* 151:930–32. [rBM]
Trevarthen, C. & Reddy, V. (2006) Consciousness in infants. In: *The Blackwell companion to consciousness*, ed. M. Velmans & S. Schneider, pp. 41–57. Blackwell. [aBM]
Tronick, E. Z. & Cohn, J. F. (1989) Infant-mother face-to-face interaction: Age and gender differences in coordination and the occurrence of miscoordination. *Child Development* 60:85–92. [CI]
Tyrrell, T. (1993) *Computational mechanisms for action selection*. Doctoral dissertation, Centre for Cognitive Science, University of Edinburgh. [aBM]
Ugolini, G. (1995) The specificity of rabies virus as a transneuronal tracer of motor networks: Transfer from hypoglossal motoneurons to connected second-order and higher order central nervous system cell groyups. *Journal of Comparative Neurology* 356:457–80. [aBM]
Ulfig, N., Neudorfer, F. & Bohl, J. (2000) Transient structures of the human fetal brain: Subplate, thalamic reticular complex, ganglionic eminence. *Histology and Histopathology* 15(3):771–90. [KJSA]
Ungless, M. A., Magill, P. J. & Bolam, J. P. (2004) Uniform inhibition of dopamine neurons in the ventral tegmental area by aversive stimuli. *Science* 303: 2040–42. [FA]
Valentine, D. E. & Moss, C. F. (1997) Spatially selective auditory responses in the superior colliculus of the echolocating bat. *Journal of Neuroscience* 17: 1720–33. [aBM]
Vanderwolf, C. H., Kolb, B. & Cooley, R. K. (1978) Behavior of the rat after removal of the neocortex and hippocampal formation. *Journal of Comparative and Physiological Psychology* 92:156–75. [aBM]
van Hooff, J. A. R. A. M. (1972) A comparative approach to the phylogeny of laughter and smile. In: *Nonverbal communication*, ed. R. A. Hinde, pp. 209–41. Cambridge University Press. [aBM]
Van Honk, J. & Schutter, D. J. L. G. (2005) Dynamic brain systems in quest for emotional homeostasis. *Behavioral and Brain Sciences* 28:220–21. [JvH]
Van Opstal, A. J., Hepp, K., Suzuki, Y. & Henn, V. (1995) Influence of eye position on activity in monkey superior colliculus. *Journal of Neurophysiology* 74:1539–1610. [aBM]
van Riezen, H. & Leonard, B. E. (1990) Effects of psychotropic drugs on the behavior and neurochemistry of olfactory bulbectomized rats. *Pharmacological Therapeutics* 47:21–34. [WJF]
Varela, F., Lachaux, J. P., Rodriguez, E. & Martinerie, J. (2001) The brainweb: Phase synchronization and large-scale integration. *Nature Reviews Neuroscience* 2(4):229–39. [SMD]
Vetter, P., Goodbody, S. J. & Wolpert, D. M. (1999) Evidence for an eye-centered spherical representation of the visuomotor map. *Journal of Neurophysiology* 81:935–39. [aBM]
von Holst, E. & Mittelstaedt, H. (1950) Das Reafferenzprincip (Wechselwirkungen zwischen Zentralnervensystem und Peripherie). *Naturwissenschaften* 37: 464–76. [aBM]
Vroomen, J. & de Gelder, B. (2003) Visual motion influences the contingent auditory motion aftereffect. *Psychological Science* 14:357–61. [EM]
Waelti, P., Dickinson, A. & Schultz, W. (2001) Dopamine responses comply with basic assumptions of formal learning theory. *Nature* 412:43–48. [FA]
Waitzman, D. M., Silakov, V. L, DePalma-Bowles, S. & Ayers, A. S. (2000) Effects of reversible inactivation of the primate mesencephalic reticular formation. II. Hypometric vertical saccades. *Journal of Neurophysiology* 83:2285–99. [aBM]
Waleszczyk, W. J., Wang, C., Burke, W. & Dreher, B. (1999) Velocity response profiles of collicular neurons: Parallel and convergent visual information channels. *Neuroscience* 93:1063–76. [rBM]
Walker, M. P., Ayre, G. A., Cummings, J. L., Wesnes, K., McKeith, I. G., O'Brien, J. T. & Ballard, C. G. (2000) Quantifying fluctuation in dementia with Lewy bodies, Alzheimer's disease and Vascular dementia. *Neurology* 54:1616–25. [DC]
Wall, P. D. (1996) Response to editorial by Anand and Craig. *Pain* 66:209. [KJSA]
(1997) Do fetuses feel pain? Definition of pain needs clarification. *British Medical Journal* 314(7088):1201. [KJSA]
Wallace, S. F., Rosenquist, A. C. & Sprague, J. M. (1989) Recovery from cortical blindness mediated by destruction of nontectotectal fibers in the commissure of the superior colliculus in the cat. *Journal of Comparative Neurology* 284:429–50. [aBM]
(1990) Ibotenic acid lesions of the lateral substantia nigra restore visual orientation behavior in the hemianopic cat. *Journal of Comparative Neurology* 296:222–52. [aBM]
Wang, S. & Redgrave, P. (1997) Microinjections of muscimol into lateral superior colliculus disrupt orienting and oral movements in the formalin model of pain. *Neuroscience* 81:967–88. [aBM]
Wang, S., Wang, H., Niemi-Junkola, U., Westby, G. W. M., McHaffie, J. G., Stein, B. E. & Redgrave, P. (2000) Parallel analyses of nociceptive neurones in rat superior colliculus by using c-fos immunohistochemistry and electrophysiology under different conditions of anaesthesia. *Journal of Comparative Neurology* 425:599–615. [rBM]
Watkins, S., Shams, L., Tanaka, S., Haynes, J. D. & Rees, G. (2006) Sound alters activity in human V1 in association with illusory visual perception. *Neuroimage* 31(3):1247–56. [aBM, SW]
Watt, D. F. (1998) Affective neuroscience and extended reticular thalamic activating system theories of consciousness. Target Article, Association for the Scientific Study of Consciousness (ASSC) Electronic Seminar. http://server.phil.vt.edu/assc/esem4.html. [DFW]
(2000) The centrencephalon and thalamocortical integration: Neglected contributions of periaqueductal gray. *Consciousness and Emotion* 1:91–114. [aBM]
Watt, D. F. & Pincus, D .I. (2004) Neural substrates of consciousness: Implications for clinical psychiatry. In: *Textbook of biological psychiatry*, ed. J. Paanksepp, pp. 75–110. Wiley. [aBM, JP, DFW]
Webster, M. J., Bachevalier, J. & Ungerleider, L. G. (1993) Subcortical connections of inferior temporal areas TE and TEO in macaque monkeys. *Journal of Comparative Neurology* 335:73–91. [aBM]
Webster's Third New International Dictionary of the English language unabridged (1961) ed. P. Babcock Gove. 1993 reprint. Könemann. [aBM]
Weddell, R. A. (2004) Subcortical modulation of spatial attention including evidence that the Sprague effect extends to man. *Brain and Cognition* 55: 497–506. [arBM, SW]
Weiskrantz, L. (1996) Blindsight revisited. *Current Opinion in Neurobiology* 6:215–20. [R-PB]
(1997) *Consciousness lost and found: A neuropsychological exploration*. Oxford University Press. [SW]
(2004) Blindsight. In: *The Oxford companion to the mind*, ed. R. L. Gregory, pp. 108–110. Oxford University Press. [RBG]
Weiskrantz, L., Sanders, M. D. & Marshall, J. (1974) Visual capacity in the hemianopic field following a restricted cortical ablation. *Brain* 97:709–28. [JS]
Weller, R. E. (1988) Vision within extrageniculate striate systems. *Progress in Brain Research* 75:293–306. [rBM]
Wentzel, P. R., De Zeeuw, C. I., Holstege, J. C. & Gerrits, N. M. (1995) Inhibitory synaptic inputs to the oculomotor nucleus from vestibulo-ocular-reflex-related nuclei in the rabbit. *Neuroscience* 65:161–74. [aBM]
Werner, W., Dannenberg, S. & Hoffmann, P. (1997) Arm-movement-related neurons in the primate superior colliculus and underlying reticular formation: Comparison of neuronal activity with EMGs of muscles of the shoulder, arm and trunk during reaching. *Experimental Brain Research* 115:191–205. [aBM]
Whishaw, I. Q. (1990) The decorticate rat. In: *The cerebral cortex of the rat*, ed. B. Kolb & R. C. Tees, pp. 239–67. MIT Press. [aBM]
Whishaw, I. Q. & Kolb, B. (1983) Can male decorticate rats copulate? *Behavioral Neuroscience* 97:270–79. [rBM]

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press

(1985) The mating movements of male decorticate rats: Evidence for subcortically generated movements by the male but regulation of approaches by the female. *Behavioural Brain Research* 17:171–91. [aBM]
(1988) Sparing of skilled forelimb reaching and corticospinal projections after neonatal motor cortex removal or hemidecortication in the rat: Support for the Kennard doctrine. *Brain Research* 451:97–114. [aBM]
Whishaw, I. Q., Schallert, T. & Kolb, B. (1981) An analysis of feeding and sensorimotor abilities of rats after decortication. *Journal of Comparative and Physiological Psychology* 95:85–103. [rBM]
Wiberg, M. (1992) Reciprocal connections between the periaqueductal gray matter and other somatosensory regions of the cat midbrain: A possible mechanism of pain inhibition. *Uppsala Journal of Medical Science* 97:37–47. [aBM]
Wicht, H. (1996) The brains of lampreys and hagfishes: Characteristics, characters, and comparisons. *Brain, Behavior and Evolution* 48:248–61. [aBM]
Wicht, H. & Northcutt, R. G. (1992) The forebrain of the pacific hagfish: A cladistic reconstruction of the ancestral craniate forebrain. *Brain, Behavior and Evolution* 40:25–64. [aBM]
Williams, C. (2005) Framing the fetus in medical work: Rituals and practices. *Social Science and Medicine* 60(9):2085–95. [KJSA]
Wilson, S. A. K. (1925) Disorders of motility and muscle tone with special reference to the corpus striatum (Croonian Lectures). *Lancet* 2:215–91. [TJP]
Windle, W. F. & Baxter, R. E. (1936) Development of reflex mechanisms in the spinal cord of albino rat embryos. Correlations between structure and function, and comparisons with the cat and the chick. *Journal of Comparative Neurology* 63:189–209. [aBM]
Winkielman, P. & Berridge, K. (2004) Unconscious emotion. *Current Directions in Psychological Science* 13:120–23. [CI]
Winn, P. (1998) Frontal syndrome as a consequence of lesions in the pedunculopontine tegmental nucleus: A short theoretical review. *Brain Research Bulletin* 47:551–63. [aBM]
Wintour, E. M., Lewitt, M., McFarlane, A., Moritz, K., Potocnik, S., Rees, S. & Tangalakis, K. (1996) Experimental hydranencephaly in the ovine fetus. *Acta Neuropathologica (Berlin)* 91:537–44. [aBM]
Woods, J. W. (1964) Behavior of chronic decerebrate rats. *Journal of Neurophysiology* 27:635–44. [aBM]
Wunderlich, K., Schneider, K. A. & Kastner, S. (2005) Neural correlates of binocular rivalry in the human lateral geniculate nucleus. *Nature Neuroscience* 8(11):1595–602. [SW]
Wurtz, R. H. & Albano, J. E. (1980) Visual-motor function of the primate superior colliculus. *Annual Review of Neuroscience* 3:189–226. [FA]
Wurtz, R. H. & Mohler, C. W. (1974) Selection of visual targets for the initiation of saccadic eye movements. *Brain Research* 71:209–14. [aBM]
Yamashita, M., Mori, T., Nagata, K., Yeh, J. Z. & Narahashi, T. (2005) Isoflurane modulation of neuronal nicotinic acetylcholine receptors expressed in human embryonic kidney cells. *Anesthesiology* 102:76–84. [DC]
Yarrow, K., Johnson, H., Haggard, P. & Rothwell, J. C. (2004) Consistent chronostasis effects across saccade categories imply a subcortical efferent trigger. *Journal of Cognitive Neuroscience* 16:839–47. [aBM]
Yuge, T. & Kaga, K. (1998) Brain functions of an infant with hydranencephaly revealed by auditory evoked potentials. *International Journal of Pediatric Otorhinolaryngology* 45:91–95. [aBM]
Zadeh, L. A. & Kacprzyk, J., eds. (1992) *Fuzzy logic for the management of uncertainty.* Wiley. [RAG]
Zahavi, D. (2005) *Subjectivity and selfhood*. MIT Press. [GN]
Zahm, D. S. (2006) The evolving theory of basal forebrain functional-anatomical "macrosystems." *Neuroscience and Biobehavioral Reviews* 30: 148–72. [aBM]
Zajonc, R. B. (1980) Feeling and thinking: Preferences need no inferences. *American Psychologist* 35:151–75. [CI]
Zelazo, P. D. (1999) Language, levels of consciousness, and the development of intentional action. In: *Developing theories of intention: Social understanding and self-control*, ed. P. D. Zelazo, J. W. Astington & D. R. Olson, pp. 95–117. Erlbaum. [AM]
(2004) The development of conscious control in childhood. *Trends in Cognitive Sciences* 8(1):12–17. [KJSA]
Zella, J. C., Brugge, J. F. & Schnupp, J. W. H. (2001) Passive eye displacement alters auditory spatial receptive fields of cat superior colliculus neurons. *Nature Neuroscience* 4:1167–69. [aBM]
Zeman, A. (2001) Consciousness. *Brain* 124:1263–89. [AMLC]
Zhang, K., Grady, C. J., Tsapakis, E. M., Andersen, S. L., Tarazi, F. I. & Baldessarini, R. J. (2004) Regulation of working memory by dopamine D4 receptor in rats. *Neuropsychopharmacology* 29:1648–55. [FA]
Zhu, J. J. & Lo, F. S. (2000) Recurrent inhibitory circuitry in the deep layers of the rabbit superior colliculus. *Journal of Physiology* 523:731–40. [aBM]
Ziabreva, I., Ballard, C. G., Aarsland, D., Larsen, J. P., McKeith, I. G., Perry, R. H. & Perry, E. K. (2006) Lewy body disease: Thalamic cholinergic activity related to dementia and parkinsonism. *Neurobiology of Aging* 27:433–38. [DC]
Zompa, I. C. & Dubuc, R. (1996) A mesencephalic relay for visual inputs to reticulospinal neurones in lampreys. *Brain Research* 718:221–27. [aBM]

https://doi.org/10.1017/S0140525X07001069 Published online by Cambridge University Press