numerals were occasionally exchanged by the computer, immediately after she correctly selected the lowest numeral in a given series (Biro & Matsuzawa 1999). Her accuracy dropped to 45% in these "switch" trials as compared to 95% correct in the normal background trials. These indicate that Ai planned a trajectory for a correct response; however, when the first and former "second" numerals were relatively distant from each other, she made on-line adjustments to the spatially exchanged stimuli.

Glover attributes the human planning system to the presence of an enlarged parietal lobe, hand preference, and tool-use. The latter two were once thought of as being unique to humans (sects. 1.2.1 and 3.1.1). We now know that a wide variety of tools is used by chimpanzees (Whiten et al. 1999). Recent studies revealed that chimpanzees exhibit preferential use of the right hand in gestural communication (Hopkins & Cantero 2003). These findings may not contradict Glover's speculation. However, future comparative studies will be needed to clarify the contributions of hand preference and tool-use to the evolution of a planning system. These should be conducted by comparing great apes that exhibit neither tool-use nor hand preference (e.g., gorillas), and those that use tools but have no hand preference (e.g., orangutans) (van Schaik et al. 2003).

In summary, whereas planning may rely on phylogenetically newer regions in the inferior parietal lobe along with the frontal lobes and basal ganglia, chimpanzees, but not monkeys, seem to share this advanced behavior.

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Form follows function in visual information processing

Richard Latto

Department of Psychology, University of Liverpool, Liverpool, L69 7ZA, United Kingdom. **latto@liverpool.ac.uk**
http://www.liv.ac.uk/Psychology/DeptInfo/StaffProfile/RMLatto.html

Abstract: Understanding neural anatomy and physiology depends on first understanding the behaviour being mediated. Glover, in his review of earlier work suggesting various dichotomies in visual processing, shows how there is a tendency to oversimplification if this approach is ignored. His own new proposals demonstrate the advantages of allowing function to drive anatomical analysis. Nevertheless, the new planning–control dichotomy he proposes, though a valuable advance, is itself an oversimplification of what must be a multi-channel system.

A particular visual function can be present only if there is a physical mechanism present in the brain to mediate it. However, it is the visual function, or rather the behaviour dependent on that function, that is selected for by evolution. Put simplistically, a physical mutation in the structure of the brain will only be selected for if it facilitates a behavioural capacity that enhances survival. Glover provides a possible example of this in his suggestion that the phylogenetically newer cortex in the human inferior parietal lobule, not present in the monkey brain, has evolved to mediate a planning function in motor control (sect. 1.2.1 and 3.1.1).[1]

A similar argument applies to environmentally modulated developmental processes. A world full of vertical lines will, through the continual processing of those lines, lead to a different neural structure from a world full of horizontal lines (Blakemore & Cooper 1970). So in a real sense, in both evolution and development, the function of the brain determines its structure. Form follows function.

The significance of this is that an understanding of behaviour is essential, and arguably has to precede, an understanding of the structure of the brain mediating that behaviour. The term *behavioural neuroanatomy*[2] perhaps best encompasses this approach. Glover's article is an excellent illustration of the value of using behaviour to drive a neuroanatomical analysis. By beginning with a historical review of motor control, he focuses the subsequent anatomical analysis on meaningful possibilities. Having presented evidence for the existence of a separate planning function that is independent of on-line motor control, he then looks at the neuroanatomical evidence to find where it might be mediated.

This, as Glover's review demonstrates, is a very different approach from some of the earlier work, particularly lesion studies, looking at the link between anatomy and behaviour. The emphasis in this earlier work tended, probably necessarily because of our limited knowledge at the time of both anatomy and behaviour, to be on rather open-ended searches for a behavioural deficit, ideally achieving a double dissociation of lesion and deficit to control for nonspecific effects (Teuber 1955). The dichotomy in visual processing between the "what" of the cortical pathway and the "where" of the retino-collicular pathway proposed by Schneider (1969) was an influential example of this approach. This emphasis on the binary division of visual behaviour continued with the subsequent subdivision of primate cortical systems into their own "what" – ventral – and "where" – dorsal – pathways (Ungerleider & Mishkin 1982). This was subsequently refined into the "perception for recognition," ventral and "perception for action," dorsal pathways of Goodale and Milner (1992). Now, Glover, very convincingly, proposes a binary sub-division of the dorsal pathway into separate planning & control systems with distinct visual inputs. So we have a binary cascade model of scientific advance with a significant division roughly every ten years (Fig. 1).

Binary subdivisions are a powerful way of getting to specifics, as anyone who has played the party game of finding a secretly chosen word in a dictionary by this means will know, but does it create an accurate description of the behavioural neuroanatomy of the brain? It fits well with the experimental designs most commonly used, for example, double dissociations, and this may be one of the reasons it is so common. We like to compare things and divide them into two categories.[3] Many behavioural studies are deliberately designed to discriminate between just two alternatives. This can be fruitful, as in the present case, but it usually leads to oversimplifications of the actual picture. Particular problems arise when there are sets of overlapping binary divisions that do not integrate easily. One of many possible examples of this in the motor control area is line bisection in neglect patients. There is good evidence that visual information feeding this relatively simple task both varies according to whether the line is in peripersonal or extrapersonal space (Cowey et al. 1994; 1999) and also depending on whether the patient is using a stick or a laser to indicate the line centre (Pegna et al. 2001). Another example is the differential role of subcortical and cortical oculomotor systems in practised (predominantly superior colliculus) and unpractised (frontal eye-fields) visual search (Latto 1978a; 1978b). As far as I can see, these various binary subdivisions do not map in a simple way onto the control-planning model.

The alternative approach is much more complex. It involves producing a global model of motor control that can then be mapped on to the neuroanatomy. This kind of approach is beginning to be fruitful in visual perception with attempts to link the modularity of processing to anatomical modularity (Livingstone & Hubel 1988; Zeki 1978). However, it is probably a little way off in our attempts to explain visuomotor processes. Meanwhile, we have to move forward in a more piecemeal way through insightful articles like the present one, always bearing in mind that the ultimate explanation will be a multifactorial one, with the nature of the neural processing driven by the needs of the outcome. Form follows function and there will be as many different neural systems, and visual inputs to those systems, as there are different kinds of motor outputs.

NOTES

1. It is perhaps worth noting that it seems unlikely that nonhuman primates do not have some element of planning in their motor control and that neural mechanisms in the frontal lobes, particularly the frontal eye-fields, have been suggested in this context (Collin et al. 1982; Latto 1986).

2. The first usage of this useful term that I can find is Mesulam (1985; 1989).

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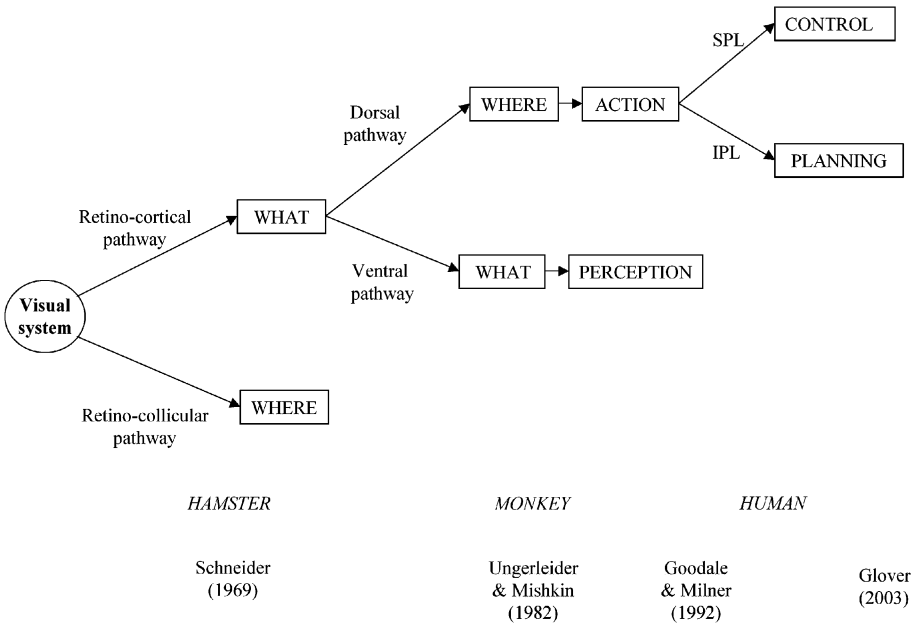


Figure 1 (Latto). The binary cascade model of the development of our understanding of the organisation of the visual system.

3. The fact that English has a specific part of speech, the comparative inflection of the adjective, to identify a binary category (higher, lower, etc.) raises the possibility that the tendency to form binary subdivisions is a fundamental process in human thought. Maybe, as with some primitive counting systems ("one, two, many"), two subdivisions are as many specific categories as we can easily cope with.

Automaticity and inhibition in action planning

Matthew R. Longo and Bennett I. Bertenthal

Department of Psychology, University of Chicago, Chicago, IL 60637.
mlongo@uchicago.edu **bertenthal@uchicago.edu**
http://home.uchicago.edu/~mlongo
www.ccp.uchicago.edu/~bbertent

Abstract: We question the generalizability of Glover's model because it fails to distinguish between different forms of planning. The highly controlled experimental situations on which this model is based, do not reflect some important factors that contribute to planning. We discuss several classes of action that seem to imply distinct planning mechanisms, questioning Glover's postulation of a single "planning system."

Glover characterizes planning as a discrete and monolithic system operating, to a large extent, prior to the initiation of an action. While this model is a welcome addition to recent models distinguishing perception and action, we believe that the mechanisms underlying planning may be much more diverse than suggested by the target article. Humans are unquestionably adept at planning skillful action, yet this function need not be meditated by a single system any more than memory, say, need consist of a single mechanism. The mechanisms underlying planning in the highly controlled experimental situations cited in support of the planning–control model do not do justice to the full diversity and complexity of human action. It has been noted, for example, that apraxic patients demonstrate strikingly few difficulties interacting with objects in naturalistic situations even as they fail completely to demonstrate such ability in controlled laboratory situations (see Cubelli & Della Sala 1996). It is important to further differentiate the construct of planning if the planning–control model is to generalize beyond simple actions involving pointing, reaching, and grasping at isolated objects.

One important distinction made by researchers in diverse fields is that between direct and mediated actions. The former category assumes a direct mapping between perception and action, whereas the latter assumes that action is mediated by stored representations. Glover emphasizes the role of mediated actions, focusing on the relation of so-called visuokinesthetic engrams in the inferior parietal lobe (IPL) to planning (sect. 4.1.1, para. 4). In addition to the evidence he cites, such representational mediation is implied by patients with visuo-imitative apraxia who are able to imitate familiar but not unfamiliar gestures (Goldenberg & Hagmann 1997). Patients with so-called *pantomime agnosia,* on the other hand, are able to imitate gestures that they are unable to recognize (Rothi et al. 1986), implying a separate pathway from perception to action that bypasses stored representations used by patients with visuo-imitative apraxia. To account for such dissociations, recent models of deficits in apraxia (e.g., Cubelli et al. 2000; Rothi et al. 1991) have found it necessary to include multiple pathways from perception to action. There is no place for a single "planning system" in these models. Rather, planning is conceptualized as consisting of multiple and diverse neural circuits that differentially contribute as a function of task, context, experience, and the available control and coordination of the relevant actions.

Some researchers have also distinguished between actions that are externally versus internally motivated, the former made in response to some distal cue, the latter generated volitionally by the subject on the basis of stored representations. These two types of behavior are mediated largely by distinct lateral and medial premotor systems respectively (Goldberg 1985; 1987; Passingham 1993).

A related distinction is that between automatic and volitional actions. In some cases, perceptual stimuli seem to elicit corresponding action plans automatically. Rizzolatti and colleagues, for example, have identified neurons in the monkey's premotor cortex that code goal-directed actions and are also activated visually by objects affording that action ("canonical neurons"; Rizzolatti et al. 1988) or by the same action being performed by the experimenter ("mirror neurons"; di Pellegrino et al. 1992). Recent behavioral studies in humans have demonstrated similar effects. Gentilucci (2002), for example, has demonstrated that the affordances of task-irrelevant objects systematically influence reach

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