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Précis of *Neuroconstructivism: How the Brain Constructs Cognition*

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Abstract: *Neuroconstructivism: How the Brain Constructs Cognition* proposes a unifying framework for the study of cognitive development that brings together (1) constructivism (which views development as the progressive elaboration of increasingly complex structures), (2) cognitive neuroscience (which aims to understand the neural mechanisms underlying behavior), and (3) computational modeling (which proposes formal and explicit specifications of information processing). The guiding principle of our approach is *context dependence*, within and (in contrast to Marr [1982]) between levels of organization. We propose that three mechanisms guide the emergence of representations: competition, cooperation, and chronotopy; which themselves allow for two central processes: proactivity and progressive specialization. We suggest that the main outcome of development is partial representations, distributed across distinct functional circuits. This framework is derived by examining development at the level of single neurons, brain systems, and whole organisms. We use the terms *encellment*, *embrainment*, and *embodiment* to describe the higher-level contextual influences that act at each of these levels of organization. To illustrate these mechanisms in operation we provide case studies in early visual perception, infant habituation, phonological development, and object representations in infancy. Three further case studies are concerned with interactions between levels of explanation: social development, atypical development and within that, developmental dyslexia. We conclude that cognitive development arises from a dynamic, contextual change in embodied neural structures leading to partial representations across multiple brain regions and timescales, in response to proactively specified physical and social environment.

Keywords: brain; cognition; development; constructivism; embodiment

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1. Introduction

Neuroconstructivism draws on three traditions. The first is the constructivist view of development attributed to Piaget and his contemporaries, such as the developmental biologist Waddington. "Neuro" introduces the second tradition: a commitment to view psychological development as entwined with the mechanistic and morphological aspects of brain development, from cell to brain to body. Third is computational modeling, which forces process theories to be explicit about the nature of information processing, resulting in a level of specification that eludes traditional, verbal, descriptive theories. Two recent books brought two of these three traditions together. *Rethinking innateness* (Elman et al. 1996) argued for a connectionist modeling approach to understanding brain and cognitive development. In contrast, *A dynamic systems approach to the development of cognition and action* (Thelen & Smith 1994) emphasized development as occurring in the context of embodiment. In *Neuroconstructivism, volume 1: How the brain constructs cognition* (Mareschal et al. 2007a), we add a focus on neural development and the development of representations.

Neuroconstructivism[1] emphasizes the interrelation between brain development and cognitive development. We see constructivist development as a progressive increase in the complexity of representations, with the consequence that new competences can develop based on earlier, simpler ones. This increase in representational complexity is realized in the brain by a progressive elaboration of cortical structures. Thus, while other constructivist theories have emphasized the notion of hierarchical integration of *knowledge* (e.g., Karmiloff-Smith 1992; Piaget 1970), we explore the relationship between the elaboration of knowledge and the development of new cognitive abilities. We assert that increases in representational complexity arise as a natural consequence of the processes of adaptation typical of complex biological systems like the brain (for related views see Mareschal & Shultz 1996; Quartz & Sejnowski 1997; Shultz 2003). Neuroconstructivism implies the

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creation of genuinely new cognitive abilities and not just the better use of preexisting abilities.

While our focus is on the development of mental representations, these develop in a physical and social environment. The body, which changes substantially during infancy, constrains what the infant can experience, process, and do. This, in turn, constrains possible learning and development. For example, the limited visual acuity of babies helps simplify the visual environment, and could also help with the integration of modalities as the clearest objects are those within reach. Physical constraints on action also force a "starting small" situation, whereby the child learns simpler effective behavior before being able to acquire more complex abilities. The social environment also constrains what and how the child will learn. The use of *motherese*, for instance, simplifies the linguistic input early in language acquisition. Indeed, most human societies engage in a process of gradually exposing infants and children to the kinds of problems that they will need to master in order to survive.

The guiding principle behind our approach is *context dependence*. Representations in the brain do not emerge or function in isolation, but within the context of cooccurring molecular, neural, bodily, and social events. This constrains and guides emerging representation through three mechanisms: *cooperation*, *competition*, and *chronotopy* (see section 2.4). The mechanisms take different forms at the different levels of implementation, but together they enable two central developmental processes: *proactivity*, which is concerned with the role of internally generated activity in the development of function, and *progressive specialization*, the fact that functions exhibit a progressive restriction of fate by becoming more specific and less plastic.

We argue that the outcome of these developmental mechanisms and processes are *partial representations*. The brain acquires and develops multiple, fragmentary representations that are just sufficient for on-the-fly processing. The role of developmental psychology is to understand how and why such partial representations emerge, how they interact, and how flexibile their configuration is.

One novel aspect of our approach is that our emphasis on *context* requires consistency among levels of explanation. We view cognitive functions as inextricably linked to their neural implementation and to the dynamic environments in which they emerge and operate, with interactions going both ways across levels. As far as *explaining* cognitive development, we see little merit in theories or models that fit data at one level, however well, yet contradict what is known at other levels. Thus, we argue for a radical rejection of Marr's (1982) independent levels of analysis argument. While explanations can be formulated independently at different levels of description, those levels are not themselves independent. A consequence of our focus on consistency is parsimony. If a phenomenon can be explained at different levels using a unitary framework, then this is preferable to an alternative where different and inconsistent interpretations are used at each level.

In the next section, we lay out the foundations of neuroconstructivism, culminating with a proposed set of principles, mechanisms, and processes. Section 3 illustrates these ideas through the use of case studies in which the neuroconstructivist framework is applied to different domains of cognitive development. In a concluding section, we identify future challenges and briefly discuss *Neuroconstructivism, volume 2: Perspectives and prospects.*

2. Foundations

2.1. Encellment

The development of the nervous system is typically described as a two-stage process. Initially, coarse structure and connectivity is laid out, with little contribution from the electrical activity of neurons. Then, the firing of neurons becomes crucial in establishing the finer-grained details of connectivity. Therefore, to examine brain development at the cellular level, we need to distinguish between *context-dependent* and *activity-dependent* processes (Crowley & Katz 1999; Herrmann & Shatz 1995).

In the early stages of neural development, activity probably plays the smallest of any role in the outcome. In neurogenesis, precursor cells (neuroblasts) differentiate into neurons, glial cells, or new precursor cells. The outcome of differentiation is affected both by the lineage of the cell and, crucially, by cell-cell interactions. A new neuron then migrates to its final position, either by passive displacement (i.e., being pushed by other emerging neurons) or with the help of radial glial cells that guide neural migration. Thus, local cellular context plays a key role in the formation of neural structures.

Neural differentiation begins during, or towards the end of, migration. Axons often traverse long distances (Purves et al. 1997), facilitated by a mixture of activity-dependent and activity-independent processes. A neurite (the neuron outgrowth that will become the axon) develops protrusions that will travel in space in response to both chemical and physical extracellular events. Particular cues guide axonal growth while others impair it, and processes can seek specific target locations with a unique chemical signature (Goodman & Shatz 1993). Once in a target area, an axon forms specific connections with dendrites through competition with other dendrites and other axons. Endogenous electrical activity also plays a role in early, presynaptic neural differentiation such that early in brain development, one observes key roles for both context- and activity-dependence.

Overproduction of cells leads to programmed cell death (Oppenheim 1991). The death of a neuron is controlled by a combination of intrinsic and extrinsic factors, whereby an internal "suicide" program will be triggered or suppressed by external chemical events involved in the guidance and competition for neural differentiation through trophic factors. Crucially, neural activity appears to have a protective effect on neurons, as it reduces cell death (Ghosh et al. 1994).

Activity-dependence is one part of a feedback loop with morphology, with each affecting the other. The activity of neurons can also alter subcellular ion channels and neurotransmitter receptors, so that the response profile of a neuron is adaptive over time (Turrigiano et al. 1994). Gene expression, too, can be affected by neural activity (Armstrong & Montminy 1993). Activity-dependence also affects the connectivity between cells. A good example is the emergence of ocular dominance columns (ODCs): Preventing sensory input to one eye considerably reduces the space occupied by neurons responding to that eye, illustrating activity-dependent competition.

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Two competing theories have been proposed to explain the emergence of cortical areas. One is the *protomap* view (Rakic 1988), which suggests that neurons are predestined early in development to occupy specific functions in specific cortical areas. The second is the *protocortex* view (O'Leary & Stanfield 1989), which argues that functional areas emerge from interactions with subcortical structures and between cortical areas. Recent reviews propose a midway view in which patterns of gene expression create, at a coarse scale, cortical areas more suited to adopting particular functions as per the protomap view. However, a protocortex account better explains the emergence of function within those poorly spatially and functionally defined areas.

2.2. Embrainment

Embrainment refers to the view that functional areas of the brain emerge and exist within a context of connections to and from other functional areas. This contrasts with a view of functional brain development in which regions are presumed to mature in relative isolation of their context, and with the view that particular cognitive operations can be localized to individual regions in adults. In fact, there is substantial evidence that the functional properties of specific brain regions are highly constrained by their past and present interactions with neighboring areas.

For example, visual event-related potential (ERP)components of congenitally deaf people differ markedly from those of typical hearing participants and participants who became deaf after the age of four (Neville & Lawson 1987). Based on these findings, Neville and Lawson (1987) proposed that early (but not late) lack of auditory input allowed a reallocation of resources, such that cortical areas typically involved in auditory processing were taken over, to a degree, by visual processing. Similarly, it has been shown that the visual cortex of people blind from an early age can be activated by tactile stimuli, particularly Braille reading. In both these examples, the differentiation of the cortex into areas of functional specialization results from a developmental process and is not functionally encapsulated. If the context changes during development, then so too can the function associated with a cortical area.

There are three important questions to consider when studying the etiology of brain functions. First, does development involve *deterministic epigenesis* or *probabilistic epigenesis* (Gottlieb 2007)? With the former, the assumption is a unidirectional path between gene and brain function. With the latter, the relationship between genes, structure, and function is bidirectional and dynamic. Second, is there a direct mapping between brain structure and function, and does this change over development? The third question concerns the nature of brain plasticity, and whether the degree of plasticity changes over development.

A substantial amount of research concerned with mapping brain and behavioral development has taken a maturational viewpoint, whereby emerging behaviors are construed to reflect underlying maturing functions of isolated areas of the brain (see Diamond 1991). A tacit assumption is that the typical adult brain (and thus behavior) is prespecified in a protomap (deterministic epigenesis), with a direct mapping between structure and function. Within this view, plasticity is a special mechanism activated by brain injury. An alternative to the maturational view is the skill-learning perspective, which proposes a continuity between infancy and adulthood in the mechanisms underlying brain learning and plasticity. According to this view, plasticity is a long-lasting feature of the brain that appears to be reduced only within a context of the stable constraints that are more likely in adulthood.

The *interactive specialization* viewpoint proposes a middle ground between the previous two accounts (Johnson 2005). It proposes that brain regions develop within the context of other brain regions (embrainment), and that the functional development of brain regions is shaped in part by interregional interactions. Specifically, cortical functional brain development is characterized by a process of increased tuning, or selectivity of functions. Thus, the mapping between structures and functions can and will change during development. Within this viewpoint, plasticity is retained when a function is not yet fully specialized.

Functional cortical brain development is best described as progressive localization and progressive specialization of function, through competition and cooperation between distinct areas. Representations that emerge within a region are constrained by existing representations in functionally neighboring areas, consistent with the interactive specialization view.

2.3. Embodiment

While the distinction between mind and the physical world may have surface appeal, ethological work has revealed a much closer coupling between behavior and environment. The brain is best viewed as embedded in its environment, and not divorced from it. As at other levels of organization, the study of a specific system must involve consideration of the other systems to which it is coupled. In the case of the brain, it is unhelpful to ignore the body and the external environment.

While previous work has distinguished embodiment (the constraints of the body on the brain) from situatedness (the constraints of the environment on the agent), we use embodiment to encompass both types of interaction. Taking embodiment seriously can reveal simpler solutions to cognitive problems than would be achieved by nonembodied approaches (e.g., Webb 1994). Indeed, considering the contribution of both body and environment can reduce the purported contribution of the nervous system (Clark 1997). For some cognitive problems, parts of the solution exist in bodily constraints and environmental properties. The role of the brain is to coordinate inner and outer worlds (Ballard et al. 1997). Hence, representations are not independent from the environment; rather, they contain partial information about the environment, sufficient to support contextually specific behaviors. Representations serve to cause behaviors rather than to mirror the environment.

Clark (1997) identifies several important ways in which an embodied perspective provides benefits to cognitive research. First, it raises awareness that an important function for organisms is to harness the environment to their advantage (Hutchins 1995). Second, the planning and execution of motor actions must consider body/environment couplings (Thelen et al. 1996). Third, an embodied view stresses the online nature of information processing (Goldstein & Gigerenzer 2002), which relies on context-dependent heuristics for just-in-time adaptations. Fourth,

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an embodied perspective recognizes how elements of the environment can act as extensions of the mind, reducing cognitive load. Fifth, Clark (1997) proposes that language embeds individuals within society, allowing individuals to share representations and affect one another's behavior. In terms of development, language provides a crucial tool to guide the experiences of infants and children (Rogoff 1998; Vygotsky 1986).

Embodied models take one of two forms. In *agent modeling*, both the organism and the environment are computer simulations (e.g., Schlesinger 2004). Alternatively, researchers may use real *robots* that function in real environments. An example of this second approach is "Didabot" (Maris & te Boekhorst 1996), a simple robot that avoids objects perceived by sensors on its left and right sides, near the front. The robot has a blind spot immediately in front of it. When several Didabots were placed in an enclosed environment that contained cubes small enough to fall within the robots' blind spots, the cubes ended up in heaps at the center and periphery of the arena. This apparently complex "tidying" behavior emerged from the coupling of a simple mind (avoid obstacles), body (blind spot), and environment (cubes and other robots).

Developmental embodied cognition focuses on the codevelopment of the nervous system and the body within a dynamic environment. This has roots in ecological psychology (e.g., Gibson 1979; 1982). A key concept of this earlier work is that of *affordances*, the fact that particular stimuli invite a specific range of actions in relation to the agent's structure and skills. Recent infancy work supports the notion of action affordance in terms of representing objects (Mareschal & Bremner 2005; Mareschal & Johnson 2003). Thelen and Smith (1994) argued more generally that the interplay between thought and action is ubiquitous in infancy, consistent with Piaget's notion of early sensorimotor development (Piaget 1952). Importantly, this approach stresses how the child actively manipulates the environment, with dynamic consequences in respect to the stimulation encountered. Similarly, the onset of self-locomotion brings about such a major change in the infant's effective environment that some have argued it causes a major reorganization of cognitive structures (Campos et al. 2000).

2.4. Principles, mechanisms, and processes

A core principle of the neuroconstructivist approach is *context-dependence*. At each level of description or analysis, the function of interest depends on the context in which it is realized. Furthermore, context-dependence is particularly important for the *development* of those functions and has significant implications for the representations that emerge.

Context-dependence constrains emerging representations through three domain-general, level-independent mechanisms: *cooperation*, *competition*, and *chronotopy* (timing). The specific implementation of these mechanisms will vary depending on the level of analysis. The mechanisms themselves make possible two processes that underlie the development of representations: *proactivity* and *progressive specialization*. The outcome of these processes is the emergence of *partial representations* (Fig. 1).

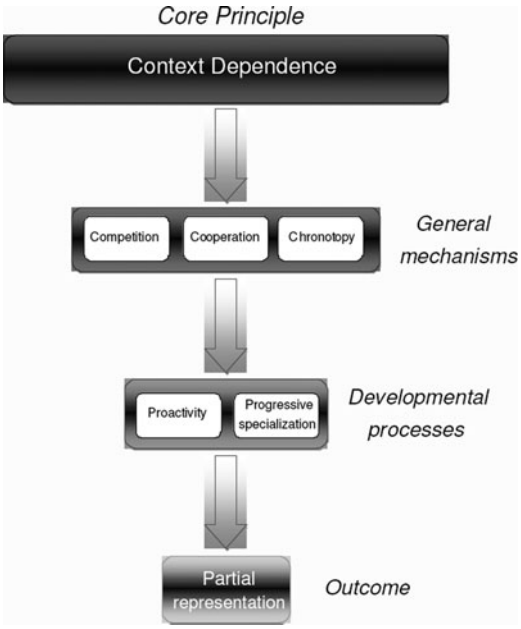


Figure 1. Principles, mechanisms and processes involved in the neuroconstructivist framework. Both the mechanisms and processes can be construed as operating at multiple levels of description.

Competition implies that from the many initial contributors to an immature function, only a subset of these will ultimately be involved in the mature function. For example, over time, the expression of gene A may prevent the expression of gene B. Similarly, inhibitory neurons or inhibitory brain structures (e.g., frontal lobe inhibition of subcortical functions) restrict competing processes from participating in a particular function. At the cognitive level, one representation of a sensory input (e.g., one view of the ambiguous Necker cube) may compete with another incompatible interpretation of the same sensory data. Overall, the purpose of competition is to allow for stable, minimal representations.

Cooperation, however, is a mechanism involved in the integration of multiple contributors to a function. For example, some genes serve as triggers for other genes, coactivity of neurons help build circuits, different brain systems may need to be simultaneously involved in a particular function, and social behavior requires cooperation among individuals. Unlike competition, but complementary to it, cooperation strives for overall efficiency through the coordination of interrelated functions. Together, competition and cooperation help build a system that may be minimal but involves a degree of redundancy that makes it relatively robust to damage.

The notion of *chronotopy* stresses that time is a dimension of development (cf. Elman et al. 1996). Some patterns of gene expression are restricted to specific developmental times, some key aspects of neural development rely on sequences of events, and adaptive plasticity occurs at different times in different parts of the developing system. At a cognitive level, this translates to saying that children will solve restricted problems grounded within a limited domain before solving abstract general problems that span several domains. Perhaps the most important temporal aspect concerns restrictions to plasticity. Neural commitment means that

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some circuits, once wired, may be hard to alter. Processing commitment, which is linked to neural commitment, means that functions become progressively entrenched and selective, and may lose sensitivity to inputs outside their current range.

Two developmental processes operate on a larger time scale than the above mechanisms. *Proactivity* refers to the idea that, at least in part, representations reflect internally generated activity. For example, spontaneous neural activity helps form certain synaptic connections. Similarly, a child initiates behaviors that have effects on the environment that, in turn, affect sensory input and ensuing behavior. We view such a feedback loop, with key involvement from a proactive child, as the engine of development. There is substantial evidence that, from an early age, infants and children are selective about the information they process from the environment (Cohen 1972; Fantz 1964; Posner 1993). There is also evidence revealing a role for spontaneously generated movements on early development (Goldfield et al. 1993; Robertson et al. 2001), even in utero (Prechtl 2001; Robertson 1988).

The other developmental process is *progressive specialization*. In its simplest form, the state of the system at any given time places constraints on future states of the system. Waddington's (1957) metaphor of an epigenetic landscape captures the idea well. According to Waddington, development is like a ball rolling down an uneven surface, able to take different directions as a function of its direction and inertia, and the landscape. Typical development would see most balls end up in the same general area of the landscape, and atypical development would see balls end up in different areas because of changes to initial direction, inertia, or landscape. A good example of such restriction-of-fate over time is phonological development. Although newborns can distinguish speech sounds from all human languages, the ability to discriminate nonnative speech sounds drops substantially after about six months (Stager & Werker 1997; Trehub 1976). Importantly, progressive specialization does not simply limit future adaptations but can also facilitate learning. In a constructivist framework, early knowledge often provides the building blocks for further knowledge.

We argue that the outcomes of these developmental processes are *partial representations*. The brain contains multiple fragmentary and partial representations that are sufficient to allow successful behavior, for example, in response to a given object over a range of contexts. Each of these is able to have an independent causal effect on behavior. This view is consistent with the distributed processing that takes place in the brain and is a computationally efficient solution to representation. New representations are thus acquired in the context of existing (also fragmentary) representations, the current effective learning environment, and the current developmental state of the body.

3. Case studies

This section presents different areas of research that serve to exemplify how our approach can be applied in different domains. We use the term *case study* in the broad sense of a focused illustration. The first four case studies are concrete examples of how the mechanisms operate. The last three cases are concerned with the notion of interactions between the different levels of explanation.

3.1. Early visual perception

Visual information processing in adults involves distinct cortical regions (Van Essen et al. 1992). For example, during object recognition, cortical processing begins in area V1 (the primary visual cortex) and progresses through a series of cortical regions until object identity per se is processed in the inferotemporal cortex. This portion of the visual system dealing with object recognition is known as the *ventral pathway* (Ungerleider & Mishkin 1982). Along this pathway early areas are involved in simpler tasks such as edge, contrast, or orientation detection (e.g., Hubel & Wiesel 1963), whereas later areas are involved in progressively more abstract representations (such as, ultimately, identifying an object). However, the pathway is not unidirectional but involves reciprocal connections between regions (Lamme & Roelfsema 2000). Later processes can affect earlier ones, such that the dynamics of information processing are more important than their specific anatomical locations (Felleman & Van Essen 1991). Each cortical region is embedded in a network of other regions and processes information in this dynamic context.

Within each region there exists competition between cells, such as that occurring through lateral inhibition. This competition occurs at each stage of processing and reflects both bottom-up stimulation and top-down biases (Desimone & Duncan 1995). Cooperation is also an important process in vision. To identify an object, it is necessary to group features of the visual input that belong to that object and to segment those from the background. This is achieved through an interactive process involving feedforward and feedback connections between the different cortical areas involved in object perception (Driver et al. 2001). Chronotopy is also important, as the functionality of the visual system emerges from a peripheral to central ordering over time (Johnson & Vecera 1996; Shrager & Johnson 1996). Later-developing neurons in higher-order areas can exploit the earlier, partial representations developed in lower, peripheral regions. Representations learned at each level constrain the representational space of subsequent levels, allowing high-order regularities to be extracted (Clark & Thornton 1997).

The input selectivity of cells involved in visual processing can be changed through learning (Desimone 1996). Moreover, experience leads to a decrease in the population of cells that respond to a familiar stimulus (Rainer & Miller 2000). Changes in performance thus reflect changes in representations, distributed across a smaller, selective population of neurons (Karni et al. 1995). Some work also reports that the cortical regions involved in a task may change as a function of expertise (Walsh et al. 1998), with fewer regions involved after learning than was initially the case (Petersen et al. 1998). This experience-dependent selectivity can enhance processing of subsets of visual inputs at the expense of other subsets. Selective attention implements a form of proactivity, whereby the child preferentially attends to some stimuli over others.

Overall, cortical regions involved in visual processing carry out contextualized intraregional competition and interregional cooperation, modulated by a degree of chronotopy that forces simpler representations to be acquired prior to progressively more complex representations. The progressive specialization at each level of processing reflects experience, which is proactive. The outcome is a set of partial representations across a

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complex network of cortical areas that together enable object recognition.

3.2. Infant habituation

Because of the limited perceptual and motor skills of infants, researchers have devised many indirect methods to assess cognitive abilities in infants. The most popular method is the use of looking-time data (e.g., Thorpe 1956). Over the repeated presentation of stimuli, babies show a progressive decrease of interest, reflected by shorter looking times to the stimuli. They are then deemed to have habituated. However, they can show renewed interest (assessed from relatively longer looking) when presented with novel stimuli. This "novelty preference" is an example of proactive exploration of the environment. By careful manipulation of how the habitual and novel stimuli differ from each other, researchers can make claims about what infants perceive to be distinct, with implications for the nature of their underlying representations (Cashon & Cohen 2000). A common approach, owing to the pioneering work of Sokolov (1963), is to suggest that a mental representation of the habitual set of stimuli is learned, and that the progressive decrease in looking time reflects an increasing match between this internal represenataion and the stimuli. Novelty preference is then taken to reflect a mismatch between the internal representation and the novel stimulus.

In accordance with our theme of consistency across levels of interpretation, Sirois and Mareschal (2002) argued that models and theories of habituation should reflect the two key neural mechanisms that support infant habituation. First, the hippocampus is involved in selective inhibition of high-order features such as color or shape (or feature relations, such as color-plus-shape) of the habitual stimuli (Nelson 1995; Sokolov & Vinogradova 1975). Hippocampal inhibition is short-lived. Hence, given that habituation has lasting effects (Zelazo et al. 1991), the second neural mechanism of habituation involves long-term storage in hippocampal-related cortical areas, notably the entorhinal cortex (Nelson 1995).

In the Habituation, autoassociation and brain (HAB) model of infant habituation (Sirois & Mareschal 2004), hippocampal and cortical functions are both implemented by simple autoassociator networks (see Sirois 2004); however, they use different learning rules to implement selective inhibition and long-term storage. Both networks are coupled through reciprocal connections and both contribute to the overall output of the system. Embedding the model in a robot and an environment illustrated how motor learning contributes to habituation performance (Sirois 2005).

The HAB model illustrates the main principles of the neuroconstructivist approach in the following ways. First, learning is driven by context, as each subsystem learns within the feedback loop of the other, antagonist subsystem. Moreover, as the robot work illustrated, habituation can be affected by motor learning. Behavior involves a mixture of cooperation (within subsystems, but also between them when their outputs are aggregated at the system level) and competition (the hippocampus attempts to shut down known input signals, whereas the cortex attempts to amplify them). Moreover, chronotopy was shown by the model's ability to capture age-related changes in performance through maturation of outward connections from the cortex (Sirois & Mareschal 2004), as observed in infant brains and in absence of prior experience. The model is proactive, as it seeks maximally stimulating input (Sirois 2005), and exhibits progressive specialization as it shifts from an initial familiarity preference to a novelty preference once known inputs are well learned. The outcome is partial representations, as the behavior of the model is achieved through the activity of several interconnected units in two distinct subsystems.

3.3. Phonological development

Infant babbling, the repetition of simple speech sounds, creates a coupling between the perception and production of language. This view is relatively recent, as early work on phonological development proposed no such connection between babbling and speech (Jakobson 1941; Lenneberg 1967).

In the first year of life, there are substantial changes to the perception of speech sounds. The best known is how infants, who are initially able to discriminate speech sounds from any human language (Eimas et al. 1971), progressively lose the ability to discriminate phonemes from outside their native language in the second half of the first year (Werker & Tees 1984). The importance of the linguistic environment is further stressed by data showing that infants' speech discrimination ability is correlated with the clarity of their mothers' speech (Liu et al. 2003).

Changes in speech-sound production can be observed in infant articulation. Before six months, most speech sounds consist of isolated vowels. However, around six months, most infants begin to babble. Articulation becomes progressively more complex over the next few months, and babbling becomes more specific to the infant's native language (Boysson-Bardies et al. 1989). This is arguably a key step towards the development of a phonological inventory, used for words and subsequently more complex linguistic structures (Vihman 2002).

The central role of auditory perception for babbling has been emphasized by research on deaf infants (Oller & Eilers 1988), who babble later than hearing infants and produce different sounds. These effects are long lasting and can negatively affect later speech (Wallace et al. 1998). Auditory feedback is thus necessary for the successful coordination of phonatory (larynx) and articulatory (vocal tract) speech systems, essential for babbling and, subsequently, speech (Koopmans-van Beinum et al. 2001).

Westermann and Miranda (2004) recently proposed a mechanistic model of the development of the link between speech perception and production. The model consists of two topographic maps, one each for articulation and perception. Within these maps, neurons responded to inputs that fell within their respective fields. The two maps were connected with Hebbian weights, such that units with high covariation between maps saw their connections strengthened and connections for units with low covariation were weakened. As a consequence, strongly covarying articulations/perceptions became prototypical; these prototypes represented vowels that could be most robustly produced based on articulatory parameters. The model's prototypical speech sounds reflected both internally generated activity and environmental input (see Vihman 1991 for a similar interpretation called the *articulatory filter hypothesis*).

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Context is central to the emergence of speech sound prototypes in both maps. Articulatory representations emerge from a dynamic interaction with perception and vice versa; moreover, these reflect the context of both internally generated and external inputs. Each topographical map implements local competition through lateral inhibition, but the coupling of articulation and perception requires the cooperation of both maps. Chronotopy is also important, as both maps require a synchronization of plasticity. Proactivity is vital, as babbling produces the coupling between perception and production. Moreover, as this coupling develops, the representations make the model progressively more selective with respect to environmental input. In real infants, in a real linguistic environment, this would lead to enhanced performance in the native language, at the expense of discrimination abilities for other languages (see also McClelland et al. 2002). Ultimately, this progressive specialization within and between maps leads to partial representations: speech sounds become activations patterns on both maps, and these cannot be isolated from one another.

3.4. Object representations in infants

Ungerleider and Mishkin (1982) proposed that object processing involves two separate cortical information processing pathways: the dorsal and ventral streams. It was proposed that the dorsal stream, terminating in the parietal cortex, processes object localization (the *where* function), whereas the ventral system, ending in the temporal cortex, performs object identification (the *what* function). The actual degree of independence of these two streams has recently been the object of some attention (Fellman & Van Essen 1991; Humphreys & Riddoch 2003; Merigan & Maunsell 1993; Puce et al. 1998). Our interest, though, is that both streams process different types of information and, as such, develop distinct representations.

The fact that object representations are, to a large degree, segregated in functionally distinct routes, implies that there needs to be a mechanism that integrates these two sources of information when they are required by some task (such as, for example, picking up a specific object from several alternatives). Mareschal et al. (1999) proposed a model that examines how these two streams of information may be gradually integrated over the course of development, explaining why successful object retrieval by infants lags behind successful visual tracking. A key assumption of the model is that both routes (ventral and dorsal) are exposed to the same input but differ in their associative learning mechanisms. The object recognition network (ventral stream) generates a spatially invariant representation of objects, using an unsupervised competitive learning rule (Foldiak 1991). The trajectory prediction network (dorsal stream) uses a partially recurrent feedforward network to track the immediately anticipated retinal position of moving objects, a proactive process. The response integration network in Mareschal et al. (1999) represents a measure of infants' abilities to coordinate and use information about the positions and identities of objects, analogous to a similar prefrontal cortical function observed in primates (Rao et al. 1997).

Interestingly, young infants show some unusual behaviors when objects are briefly occluded. For instance, infants can remember spatial properties of occluded objects but not necessarily identity features (Kaldy & Sigala 2004; Leslie et al. 1998; Simon et al. 1995; Wilcox & Schweinle 2002; Xu & Carey 1996). Object individuation at 4.5 months relies on shape and size, at 7.5 months on texture, and only at 11.5 months does it involve color (Wilcox 1999). Mareschal and Johnson (2003) examined under which conditions four-month-olds would retain position or identity information during a 5-second occlusion. They found that the functional value of objects (their affordance, in Gibsonian terms) appears to drive a competition between dorsal and ventral streams for object retention. Objects that afford the possibility of actions maintain dorsally processed information, whereas objects that do not afford action maintain ventral information.

This and other evidence highlights the contextual nature of object processing, involving the child, the environment, the affordance of objects and functionally distinct neural representations. Competition and cooperation occur at different levels in the distributed system involved in object recognition. The system also exhibits progressive specialization, in that each stream excludes irrelevant sources of information (spatial or featural) to carry out its function. Ultimately, the infant brain must coordinate partial representations in distinct systems to act on specific objects (Mareschal et al. 1999; Rao et al. 1997).

3.5. Ensocialment

The importance of the social context on cognitive development has a long history (e.g., Bandura 1986; Rogoff 1990; Vygotsky 1978). Our focus is on the developing child situated in an environment that includes other humans and in which development involves a collaboration between the child and those who support and nurture this development (Rogoff 2003). While these ideas are not new, it is only more recently that the importance of social behavior has made forays into the neurosciences (e.g., Adolphs 2003).

An early aspect of social brain function is the preference of newborns (as early as within the first hours after birth) for face-like stimuli (Johnson et al. 1991; Valenza et al. 1996). Although the specific cues that elicit the preference remain a source of debate (see Johnson 2005 for review), it has been suggested that three high-contrast blobs in the positions of the eyes and mouth may be sufficient (Johnson & Morton 1991; Morton & Johnson 1991). Hence, the brain does not contain, from birth, a detailed specification of a face but a skeletal, partial, representation. The preference for face-like stimulation makes the infant proactive in seeking stimulation with faces, which places the infant in a learning context in which other cortical systems will learn about faces. Hence, an initial bias ensures that later developing areas of the cortex acquire specific specialization for faces (Johnson 2005). Similarly, evidence shows that infants prefer to look at faces that show direct gaze towards them (Farroni et al. 2002). Maintaining eye contact with someone ensures foveation of the face, which may prove essential to the emergence of a cortical face area (Johnson 2004).

Children benefit from "ensocialment" in several other ways. For example, Vygotsky (1978) was probably the first to fully recognize the role of language in shaping cognitive development. Vygotsky argued that, cognitive change involved moving from external speech, which

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instructs the child, to private speech, whereby the child maintains an internal dialog that takes over from external instruction to guide behavior. Indeed, Berk and Gavin (1984) observed that most vocalized private speech in group settings actually takes place when a child is working alone on a difficult task.

Vygotsky (1978) further proposed that in relation to the child's current level of development, there existed a small window of optimal stimulation within which to provoke further development: the *zone of proximal development* (ZPD). Infants display this spontaneously by exhibiting a preference for stimuli that are moderately discrepant from their current knowledge or capabilities (McCall et al. 1977). Teaching below this zone provides little enhancement as it is within the child's current grasp. Similarly, teaching above this zone would also provide few gains as the child would fail to see the path between her current level of competence and the teaching. Thus, Rogoff (1990) proposed the notion of *guided participation*, whereby progress is optimal when child and teacher share a focus and purpose in learning. The main idea in terms of instruction (and, generally, pedagogy) is that it channels the child's interaction with the environment (see also Csibra & Gergely 2006). The emphasis on joint participation once again highlights the importance of proactivity from the child.

3.6. Atypical development

In most cases, the outcome of development is relatively predictable. However, how can we explain variability in developmental outcome? Some variability is observed in intelligence, much more in cases of developmental disorders. Developmental disorders can have several causes. Disorders can stem from genetic abnormalities, such as in Down syndrome, Williams syndrome, and fragile X. They can be identified on behavioral grounds, such as in autism, Specific Language Impairment (SLI), Attention Deficit Hyperactivity Disorder (ADHD), and dyslexia. In these latter cases, some genetic influence is suspected as these conditions can run in families but the genetic basis is not fully understood. Finally, disorders can be caused by atypical environments, either biochemical (e.g., mothers taking drugs during pregnancy) or psychological (e.g., cases of deprivation or abuse). Notably, some developmental disorders can exhibit very uneven cognitive profiles. For example, there may be particular problems in language but less so in nonverbal areas (e.g., SLI). Some abilities can appear relatively stronger against a background of low IQ (e.g., face recognition in Williams syndrome). How should we explain these uneven profiles?

Where uneven cognitive profiles are observed in typical adults who have experienced brain damage, the usual recourse is to infer that certain parts of the adult cognitive structure have sustained damage. Some researchers have attempted to apply this explanatory framework to developmental disorders, inferring that isolated cognitive components have *failed to develop*, while the rest of the cognitive system has developed typically. Examples include a Theory of Mind module in autism (Baron-Cohen 1999; Baron-Cohen et al. 1993) and a syntax module in SLI (Van der Lely 1997). Where the disorder has a genetic basis, there has been a further temptation to view uneven cognitive profiles as evidence for direct links between genes and particular cognitive mechanisms.

Explaining developmental deficits with reference to the typical adult cognitive system is, however, problematic. The adult structure is not prespecified but is itself a product of development. Yet strong analogies with adult brain damage produce accounts of developmental deficits with no role for development at all. In contrast empirical evidence supports the role of development in producing atypical cognitive profiles. When Paterson et al. (1999) explored the language and number abilities of toddlers with Down syndrome and Williams syndrome, they found a different relative pattern to that observed in adults with these disorders. The profile in early childhood was not a miniature version of the adult profile.

The influence of genetic variation and genetic mutation on brain development is not yet fully understood. However, current data suggest that genetic effects are typically graded and diffuse, and have not been found to co-occur with the regions of the cortex associated with specialised higher cognitive functions in typical adults. For example, the British KE family were initially identified as having a specific speech and language deficit caused by mutation to a single gene (FOXP2). However, subsequent research revealed that there were widespread structural and functional brain differences in family members possessing the mutation, while cognitive deficits extended outside the domain of language to negatively affect, for example, performance on nonverbal, rapid associative learning tasks (Watkins et al. 2002a; Watkins et al. 2002b). In a comparison of a number of genetic syndromes, Kaufmann and Moser (2000) confirmed that diffuse effects on brain development are the norm.

The neuroconstructivist approach places the developmental process at the heart of explanations of developmental disorders (Karmiloff-Smith 1998a). Empirically, the framework encourages researchers to focus on trajectories of development rather than static snapshots. Theoretically, disorders are viewed as cases of atypically constrained trajectories. A disordered system is still adaptive, yet it may not possess the neurocomputational constraints that are appropriate to acquire a domain. In some circumstances, apparently typical behaviors may be generated by atypical underlying processes (see, e.g., Deruelle et al. 1999; Karmiloff-Smith et al. 2004, for work on face recognition in Williams syndrome). In other cases, the atypical constraints may produce *better than typical* performance in a domain, such as in some aspects of perception in autism. In Waddington's (1957) metaphor, the epigenetic landscape has changed.

Several of the core ideas of neuroconstructivism are emphasized by the study of atypical development. For example, in some cases *interactive specialization* of cortical areas appears atypical. Adults with Williams syndrome exhibit face recognition skills in the normal range, but examination of ERPs reveal reduced evidence of specialization and localization of neural activity (e.g., Grice et al. 2001). Neuroimaging data have suggested differences in the constraints of *chronotypy*, in terms of the changes in connectivity (and associated plasticity) over time in disorders such as autism and Down syndrome (e.g., Becker et al. 1986; Chugani et al. 1999).

Differences in input encoding have been proposed to have *cascading effects on the context* in which other cognitive abilities are acquired (e.g., in autism, SLI, and dyslexia). Alterations in the level of abstraction achieved in forming internal representations, or in the dimensions of

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similarity that those representations encode, can play a material role in the ability of other brain systems to employ this information to drive other processes. It is possible that in autism, SLI, and dyslexia, for example, the consequence of atypical similarity structure in the input representations results in a processing deficit much higher up in a hierarchy of representational systems. Differences in *embodiment* may also impact on the trajectory of development. For example, Sieratzki and Woll (1998) proposed that in children with spinal muscular atrophy, a disorder that reduces early mobility, language development might be accelerated as a compensatory way for the young child to control their environment. Lastly, an atypical child co-specifies an *atypical social environment*, for example, in the expectations and reactions of parents and peers, which has also been observed to influence these children's development.

Of course, when we place an emphasis on development as a trajectory, and atypical development as an atypically constrained trajectory, it becomes increasingly important to specify what is different about the constraints and mechanisms of change. Here *computational modeling* has offered exciting avenues for progress in the study of disorders (e.g., disorders of infant gaze perception: Triesch et al. 2006; disorders of language: Thomas & Karmiloff-Smith, 2003).

3.7. Dyslexia

Reading is a relatively recent human invention, going back only a few thousand years. It is highly unlikely that evolution has produced domain-specific constraints on the cognitive systems involved (McCandliss et al. 2003). The existence of a specialised reading system in a brain must therefore represent an adaptation of more general functions to reflect the specific environmental demands of cultures that encourage expertise in this area.

Neuroimaging suggests that reading recruits up to a dozen distinct brain areas (Dehaene 2003). One particular area, the *visual word form area*, shows comparably high levels of activity for words and pseudowords (seemingly plausible nonwords made up of standard letters), but not for illegal letter symbols, suggesting an area that processes visual stimuli that look like words, prior to establishing whether they have a meaning (Dehaene et al. 2002; Posner et al. 1988). The location of this area is relatively consistent across individuals and languages (and thus scripts). Because it couldn't have been selected by evolution, this area must be one that happens to have appropriate computational properties for processing words; that is, fine foveal discrimination and invariant recognition of letter- and word-sized stimuli (McCandliss et al. 2003).

The emergence of reading requires a mapping to be established between the linguistic phonological discriminations of the preliterate child and the letters or letter clusters he or she must learn: That is, the child must learn the relation between graphemes (new) and phonemes (old). Some languages, such as English and French, have inconsistent mappings between graphemes and phonemes (e.g., the letter 'i' sounds different in the English words bit and bite). Compared to languages with consistent mappings (e.g., Italian and Spanish), inconsistent mappings can delay proficient grapheme-phoneme decoding by up to two years (Goswami 2002; 2003).

Reading disabilities in English affect 5 to 17 percent of school-aged children (Shaywitz & Shaywitz 1994). Two main subtypes of developmental dyslexia have been proposed (Castles & Coltheart, 1993; Manis et al. 1996). *Phonological developmental dyslexia* involves difficulties reading novel or pseudowords, whereas *surface developmental dyslexia* describes a difficulty in reading irregular words for which the pronunciation cannot be predicted from the sounds of the individual letters (words such as aisle or yacht).

Twin studies have suggested a significant genetic contribution to developmental dyslexia (Pennington 1999; Plomin & Dale 2000; Plomin & Rutter 1998). However, a direct mapping of gene to cognitive function is highly unlikely. Therefore, one might expect to observe more widespread effects than dyslexia alone if there is a genetic aetiology. Although there is no consensus and substantial variability in the literature, especially for surface dyslexia, various concurrent cognitive deficits have been observed in individuals with dyslexia, suggesting a more general sensorimotor syndrome (Stein & Walsh 1997).

Most computational models of typical and atypical reading development assume that the domain problem constitutes learning to map between the representational codes for written words, spoken words, and word meanings (e.g., Harm & Seidenberg 2004; Plaut et al. 1996; Seidenberg & McClelland 1989). Surface dyslexia has been simulated by altering the initial computational constraints so that the system's ability to learn the mapping between orthography and phonology is reduced. (Sometimes this involves impairing a putative route to pronunciation via word meaning.) Phonological dyslexia has been simulated in two majors ways. The first method is to degrade the properties of the phonological representations (e.g., Harm & Seidenberg 2004). The second method degrades the ability of the system to learn the functional linking orthography and phonology. It is notable that, in this account, similar manipulations can produce symptoms of either surface or phonological dyslexia; many people with dyslexia also show symptoms of both types (Manis et al. 1996).

Developmental dyslexia serves to illustrate the principles of neuroconstructivism in the following ways. Reading is a specialisation of a more general system, reflecting the context of a particular environment. In typical development, reading involves dynamic interactions between multiple functions with suitable computational properties. Partial representations interact during development, as highlighted by the restructuring of phonology when the mapping to graphemes is learned. In developmental dyslexia, the somewhat heterogeneous clusters of difficulties reflect the different ways crucial mappings between phonology, orthography, and semantics can be disrupted, as illustrated by computational work. This is consistent with the suggestion of a genetic aetiology, which would be unlikely to selectively disrupt a function that evolution cannot have selected in the first place. Rather, genetic anomalies are expected to show more general, diffuse effects with differential rather than specific consequences in particular domains.

4. Conclusions

Our framework has many implications for developmental theory. One major implication is that our proposal of

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multilevel isomorphism is a radical rejection of Marr (1982). Cognition cannot be studied independently of the brain and body. Another important implication is the central role of developmental trajectories in the interpretation of adult cognition. There is no teleology involved in development; mature, normative cognition is an outcome of development, not a pre-specified target (Thomas & Karmiloff-Smith 2003).

We have also argued that brain regions do not utilize complete representations. In support of this view, we discussed, first, how a particular input signal is typically processed separately along distinct dimensions (e.g., shape, color, motion in object perception), and second, that functional brain systems are interrelated with other functional systems, and are located and within a body and an environment. All these contexts provide varying levels and sources of information such that only fragments of information need to be represented. An implication is that cognition will be compositional and systematic (e.g., Fodor 1975; Fodor & Pylyshyn 1988) only if the context permits it.

Progressive specialization, and notions such as emergent modularity (e.g., Karmiloff-Smith 1998a) imply that, as a result of development, the cognitive architecture will exhibit a progressive lack of flexibility to the novel. This can be observed when emergent specialized systems have well-delineated functions (Johnson & Munakata 2005). These specialized systems should not be construed as mere imprinting from environmental pressures and regularities. The child, from birth (e.g., Robertson et al. 2004), is an active contributor to his or her development. Our emphasis on context-dependence may be taken as implying that it is impossible to make general claims about cognition. This is not the case. Instead, we argue that the key to understanding contextualised function is to identify those contexts that are central to the function of interest, while ignoring those contexts that may have a peripheral rather than central role in determining the function of interest.

A recurrent theme in our book is the need for causal theories regarding what makes complex behaviors emerge. These theories need to explain behaviors on multiple time scales. They must explain how and why behaviors unfold as we observe them in real time, as well as how they unfold in developmental time. To do this, we need more than just a very detailed description of the behaviors that can be observed at any point. Certainly, such descriptions are essential for the advancement of causal theories of development, but they are unsatisfactory to the extent that they are unable to explain or predict new behaviors. The clearest example of this is with regards to explaining the behavior of children with developmental disorders. Unless one has a mechanistic theory of what is causing behaviors to unfold, and a causal theory of what is atypical in such children's processing, it is impossible to explain or predict why one set of atypically developing children may show a delay at one behavior and excel at another, while a second set of atypically developing children will excel at the former behavior but have a developmental delay in the latter behavior.

In the companion volume, *Neuroconstructivism, volume2: Perspectives and Prospects* (Mareschal et al. 2007b), we invited nine research labs with objectives broadly consistent with the neuroconstructivist approach to present their computational modeling work. The questions the models are built to investigate differ both in the level of description and in time scale over which the relevant behaviors operate. Some models focus on relatively rapid adaptation occurring (perhaps) at the cellular level of description, whereas other models focus on relatively slow adaptation occurring at the cognitive level.

We asked all contributors to the companion volume to emphasize the following aspects of their contributions when describing their work:

What functional brain constraints operate on the process of representation development?
What embodiment or situatedness constraints operate on the process of representation development?

Ultimately, computational models are tools to help us reflect on questions of process and mechanisms. Therefore, we also asked the contributing authors to answer the following questions:

How does the model embody these constraints?
What concrete predictions does the model make?

In *Neurocontructivism, volume 1: How the brain constructs cognition*, we set out to investigate how the representations that underlie cognition emerge in the brain during development. We argued that the emergence of such representations is the outcome of a constructivist process involving constraints that operate at all levels from the cellular environment to the social environment. To truly understand how these representations emerge, it is necessary to locate our theories at the point where the constraints of brain, body, and environment come together.

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NOTE

1. We acknowledge that the term *neuroconstructivism* has been used by others previously, sometimes with a general meaning very similar to our usage (Karmiloff-Smith 1998a; Quartz & Sejnowksi 1997) and sometimes with a differing meaning (Sheridan 1997).

Open Peer Commentary

Are interactive specialization and massive redeployment compatible?

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Abstract: I offer a simple method for further investigating the Interactive Specialization framework, and some data that may or may not be compatible with the approach, depending on the precise meaning of "specialization." Findings from my lab indicate that, while networks of

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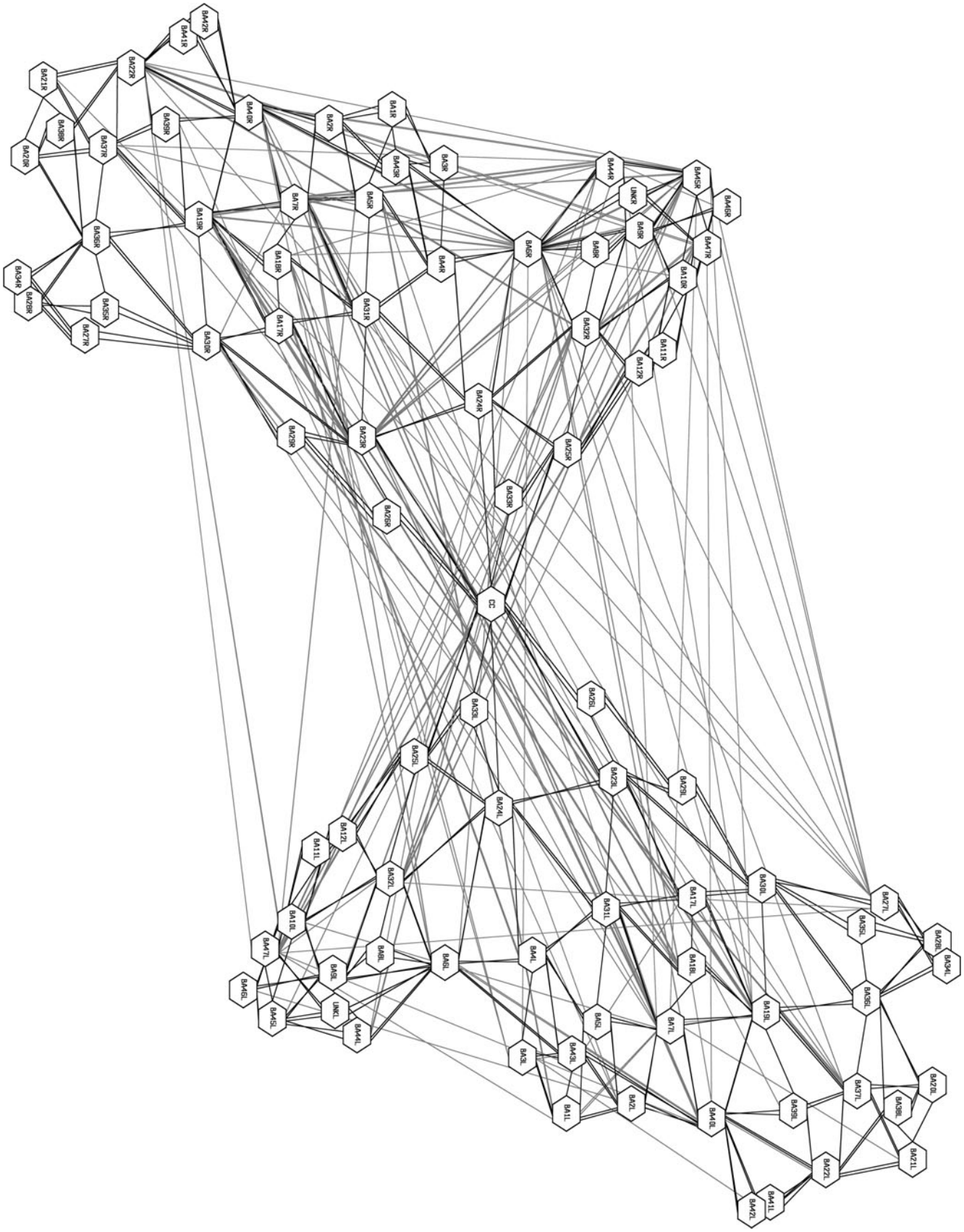


Figure 1 (Anderson). Cortex represented as adjacency + co-activation graphs. Here the Brodmann areas are nodes, with black lines between adjacent areas and gray lines between areas showing significant coactivation. The graph on the left shows coactivations from 56 action tasks, and the graph on the right shows coactivations from 77 attention tasks. Graphs rendered with aiSee v. 2.2.

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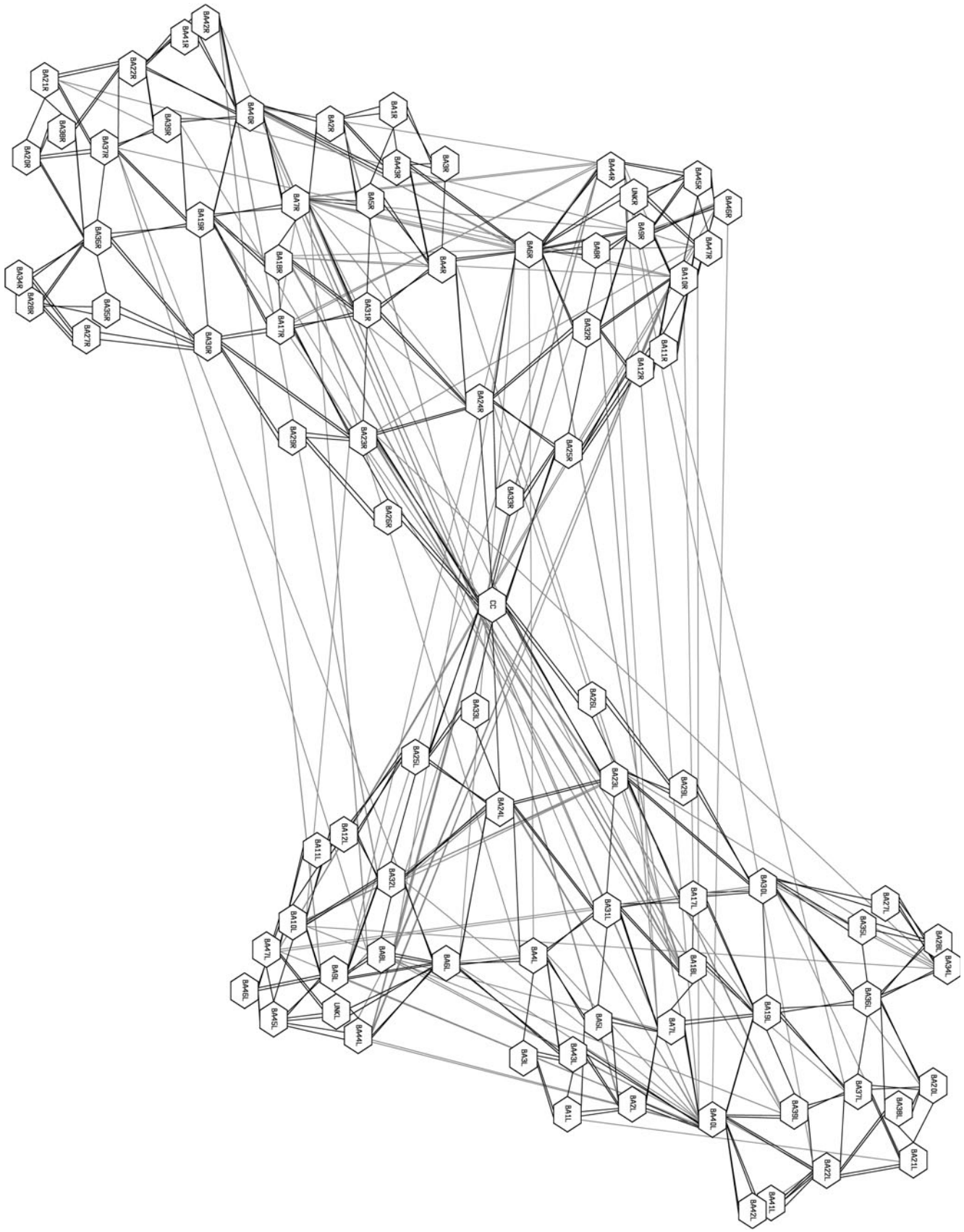


Figure 1 (Anderson). Continued.

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brain areas cooperate in specialized ways to support cognitive functions, individual brain areas participate in many such networks, in different cognitive domains.

Much as I would love to have the time and space to comment more fully on this fascinating and comprehensive book – for example, the issues of embodied cognition in general, and embodied representations in particular, are topics near and dear to my heart – I will conform to the *BBS* mold and comment on only the one aspect of the book that is most relevant to my most recent work: the framework of *Interactive Specialization* (IS). In what follows I will offer: (1) a method for investigating this framework, and (2) some data that may or may not be consistent with it (depending on what is meant by "specialization").

In contrast to localization-based approaches, which at the extreme tend to expect a 1 : 1 correspondence between cognitive functions and brain areas, the IS framework in *Neuroconstructivism, Vol. 1: How the Brain Constructs Cognition* (Mareschal et al. 2007a), treats cognitive functions as the "emergent product of interactions between different brain regions" (p. 60). For IS, the targets of functional brain mapping should be collections of cooperating neural circuits, not individual brain areas; and the focus of developmental neuroscience should be on changes in interregional connectivity, rather than on the maturation of individual regions.

I wholeheartedly applaud this shift in focus. Networks of cooperating brain regions are *prima facie* far more plausible targets of (high-level) functional attributions than are individual areas, so much so that I find it something of a puzzle that there hasn't been far more effort along these lines (which is not to imply that there has been none). I think one reason is that the techniques typically used in cooperation-focused investigations are complex, they are hard to master, and they produce results that can be difficult to interpret. Thus I would like to take a moment to outline a *very simple* analytical technique we have been using in my lab (Anderson et al., in press).

The technique involves the simple expedient of choosing a spatial segmentation of the cortex (current analyses use Brodmann areas, but any consistent segmentation scheme will work) and analyzing large numbers of fMRI studies in some specific cognitive or behavioral domain to identify statistically significant instances of coactivation. We recently compiled a database of fMRI studies containing 530 experiments in 18 cognitive domains, with the results of each experiment coded primarily in terms of which Brodmann areas contained post-subtraction activation(s). The baseline chance of activation for each area is determined by dividing the number of experiments in which it was activated by the total number of experiments in the database. Then, for each pair of Brodmann areas, we use a chi-square measure to see if their observed degree of coactivation (in a given domain) was significantly different from what would be predicted by chance. With these coactivated pairs, we also perform a binomial analysis to obtain directional information. (It is sometimes the case that, while area A and area B are coactive more (or less) often than would be predicted by chance, the effect is asymmetric, such that area B is more active when area A is active, but not the reverse.)

The results of such analyses are conveniently represented as a graph, where the nodes are Brodmann areas, and edges between the nodes indicate significant coactivation. Figure 1 shows the graphs from one such analysis, for a set of action and attention tasks. We hypothesize that the network of coactivated areas revealed by such analysis represent those areas of the cortex that cooperate to perform the cognitive tasks in the given domain.

With the data in this format, it becomes possible to formulate some very simple questions, and use some well-understood methods to answer them. For instance, in graph theory a clique is a set of fully interconnected nodes that are sparsely connected to the rest of the graph (Alba 1973). Neural cliques, which in this context represent small networks of coactive areas operating independently of other parts of the graph, seem likely to correspond to the neural components that support a set of closely related cognitive functions or subfunctions. One can also look at other features of the graphs, such as local topography, to help make plausible inferences about underlying function. For example, a hub-and-spoke pattern of coactivation may indicate broadcast or information consolidation functions; in contrast long strings of connected nodes might indicate serial processing. Since one can also look at the emergence of such structures over time, this seems an ideal tool for investigating the IS framework. The basic data for such investigations will become increasingly available as results from more longitudinal fMRI studies are released. More generally, I think that graph theory is an underutilized tool in cognitive neuroscience, and coactivation graphs in particular offer the promise of making cooperation-sensitive investigations into neural function more broadly intelligible.

This brings me to some promised data. We generated coactivation graphs in eight cognitive domains (action; attention; emotion; language; memory; mental imagery; reasoning; visual perception) from 472 experiments in our database and evaluated how much edge overlap and how much node overlap there was among the various domains. In this context, node overlaps indicate Brodmann areas that support tasks in both domains, whereas edge overlaps indicate similar patterns of cooperation. Given the focus on the developmental emergence of networks of brain areas to generate cognitive functions, the IS framework would seem to predict little edge overlap, as differences in function would presumably result from differences in interregional cooperation. This is just what we found; using Dice's coefficient as our measure ($D = 2(o_{1,2})/(n_1 + n_2)$, where o is the number of overlapping elements, and n is the total number of elements in each set) we found very little edge overlap between the domains (Mean(D) = 0.15, SD 0.04). However, we found a *great deal* of node overlap (Mean(D) = 0.81, SD 0.04). It is not clear if the IS framework is compatible with this latter finding, because Mareschal et al. do not distinguish between increasing *computational* specialization in development (whereby a given region comes to have an increasingly well-defined subfunctional role in the networks in which it participates) and *domain* specialization (whereby increasing specialization of functional networks also implies increasing dedication of participating regions to a narrow and domain-restricted range of cognitive functions). The result reported is just one among a number of findings that suggests that brain regions are *not* domain specialized entities, but in fact typically support functions across many different cognitive domains (Anderson 2007a; 2007b; 2007c). I would welcome the authors' comments and clarifications on this issue.

A good approach to neural and behavioural development but would be even better if set in a broader context

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Abstract: An attractive feature of *Neuroconstructivism, Vol. I: How the Brain Constructs Cognition* is its emphasis on the active role of the

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individual in neural and behavioural development and the importance of the interplay with the environment. Certain aspects of development are omitted, however, such as specializations for the distinctive ecologies of infancy and childhood and the scaffolding-like features of behaviour seen during development. It was also a pity that so little credit was given to many scientists who have contributed to just those aspects of development on which the authors focus.

A quiet revolution has been taking place in the thinking about the development of the nervous system and behaviour. Only 30 years ago E.O. Wilson (1976) felt able to write that development was a "module" that could be decoupled when correlating differences in genomes with differences in the adult phenotypes. Few would agree with that view nowadays. The objective to discover the relative importance of genes and the environment at the population level has a distinctly old-fashioned feel about it now, based as the approach is on the assumption that sources of variation add together. "Systems analysis" is the phrase on everybody's lips, although this particular fashion has rarely been translated into an understanding of process. What we need is a coherent way of rendering usable the intuition about the interplay between the developing organism and its environment. The two volumes, of which I shall focus on the first (Mareschal et al. 2007a), represent a serious attempt to provide such a road map.

Setting out their stall in the first volume, Mareschal et al. argue that the challenge is to incorporate information from the brain when explaining the development of behaviour without lapsing into reductionism. Quite right. As Robert Hinde put it many times, we have to cross and recross the boundaries between the different levels of analysis (Bateson 1991). The case Mareschal et al. make for some degree of formalization is that an explicit working model brings with it mental discipline and may expose easily missed weaknesses in a verbal argument. Such models can also serve several other valuable functions. They can show how we are easily misled by the dynamics of development into supposing that the processes are so complicated that they are beyond comprehension. From the point of future empirical research, they can suggest profitable new lines of enquiry. Finally, they bear directly on the general arguments about the interplay between internal and external factors. As far as linking levels of analysis is concerned, the models point to the parameters that are features of the organism as opposed to ones that might be manipulated externally by experiment. One example is the constant affecting the rate at which plastic changes occur. These hypothetical features of the organism, if real, must have some correspondence to underlying neural mechanisms.

Mareschal et al. emphasize the active role of the individual in its own development and pick out three principles which they regard as crucial: cooperation between different systems, competition, and chronotopy (by which they mean relative temporal ordering of expression). Competition is defined as the process by which one of several components wins out and becomes the relevant functional unit. Despite the high level of abstraction, I believe that they are generally correct in much of what they argue for, although I think competition has an additional side to it. By the process of competitive exclusion, experience of one kind can shut out the effects of subsequent experiences of another kind – very important in terminating sensitive periods in development.

Other important features of development are also left out of the authors' analysis. First, many manifestations of the young individual's brain and behaviour represent specializations to the particular ecological conditions of that stage of development; suckling by young mammals is one well-analysed case. Second, while I applaud the authors' emphasis on the active role of the individual, they do not draw attention to the scaffolding-like character of many instances of such behaviour; as in the assembly of a tall building, the scaffolding can be dismantled once the structure is in place. Third, the conditional responses to local circumstances mean that, viewed globally, phenotypic characteristics of adults can be extremely variable, but in each case well adapted to the particular conditions of the local environment –unless the individual has been "misinformed" by the events that initially triggered its developmental trajectory in early life (Bateson et al. 2004). Finally, despite all their plasticity, many aspects of fully developed individuals are highly robust and their development across the population is seemingly impervious to great differences in experience of individuals. We need theories of how and why.

The authors are rather more impressed with their own sense of originality than is really justified. I suspect that I will not be alone in being irritated by some of their claims that their approach is so novel. Many distinguished neuroscientists, behavioural biologists, and developmental psychobiologists who have made major contributions to the understanding of development have seemingly been air-brushed out of the picture. So for example, no references are given to the work of Andrew, Blakemore, Fentress, Gray, Griffiths, Hinde, Johnston, Konishi, Lehrman, Marler, Michel, Moore, Nottebohm, Rosenblatt, Schneirla, Oyama, Trevarthen, Rogers, Rose, and many other important figures who have shaped understanding of behavioural development. When it comes to behavioural imprinting, Gabriel Horn is mentioned but nothing is stated about his long-term collaboration with me or about the neural net model we developed together (Bateson & Horn 1994). This model was developed with precisely the same objectives as those stated by the authors of the first volume, namely aiming to provide an account that was plausible at both the behavioural and neural levels. We set out many important implications for development. A general characteristic of our three-layered, unsupervised model was that it exhibited a well-known feature of development, simulating the competitive exclusion process that generates a descriptive sensitive period. While tending to settle into familiar habits, it was also able to build with increasing elaboration on the basis of previous perceptual experience. It was able to classify together different views of the same object and simulated well the perceptual learning process by which low stimulus value cues become more salient as a result of being paired with high stimulus value cues.

The authors argue admirably for a multidisciplined approach to the study of brain and behavioural development. It is pity, therefore, that they have seemed to settle into a silo of their own making and have not drawn more explicitly on many of the important conceptual and empirical advances in subjects close to their own. It shows how much more dialogue is necessary if the cooperation needed for the enterprise in which they are engaged is to proceed satisfactorily in the future.

Unimodal experience constrains while multisensory experiences enrich cognitive construction

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Abstract: Mareschal and his colleagues argue that cognition consists of *partial representations* emerging from organismic constraints placed on information processing through development. However, any notion of

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constraints must consider *multiple sensory modalities*, and their gradual integration across development. Multisensory integration constitutes one important way in which developmental constraints may lead to *enriched representations* that serve more than immediate behavioural goals.

Neuroconstructivism, Vol. 1: How the Brain Constructs Cognition (Mareschal et al. 2007) makes a persuasive argument that we should use computational modeling tools to attempt to understand the processes of change in those neural structures that underlie cognitive development. The authors argue that modeling can help researchers understand the constraints acting on experience (and thus neural development) at multiple levels, with particular emphasis placed on the constraints of the nervous system and the body. The consideration of these multiple levels of constraint represents an important step forward, as it provides a more formal conceptualization not just of the causal processes of change in cognitive development, but also of how cognitive processes in the mature adult are constrained by developmental trajectories (see also Westermann et al. 2006).

This approach pays homage to both cognitive neuroscience and to Piaget. Cognitive development is considered on a neural and functional neural systems level (and indeed is explained as arising from causal interactions between these systems). In homage to Piaget, the authors' approach asserts that children proactively construct their own representations by means of internally generated learning processes. However, when we consider the nature of our internal representations of the world – the contents of cognition – there is a key point of divergence with Piaget. For while Piaget (1952) was concerned with the question of how infants and children construct *objective* (or in Mareschal et al.'s terms, *complete*) representations of the world, the authors of *Neuroconstructivism* argue that *partial representations* form the substrate of cognition, both during early development and in mature adults. Mareschal et al. describe partial representations as "just sufficient to allow successful behavior," (p. 16) and they justify this view of cognition on the basis that it is a by-product of learning to achieve a behavioural goal within a system possessing particular neural and embodiment constraints.

However, Mareschal and colleagues' formulation of constraints is somewhat limited. In particular, the authors neglect to consider the critical role of multiple interacting sensory modalities in development. While the authors present a number of models of learning that take different modalities as their inputs (visual, auditory, etc.), none of the models process inputs from more than one sensory modality at any given time. It should be remembered that the interaction of multiple sensory modalities was a key aspect of Piaget's constructionism. More specifically, Piaget argued that the initial steps toward objectivity in infants' representations of their world were achieved in part through the integration of separate, modality-specific schemas (Piaget 1953). In the following observation, Piaget notes what he termed the "organisation of reciprocal assimilation," when, for the first time, his 4-month-old daughter watches herself grasping an object:

> Observation 68. – At 0;4 (9) Lucienne makes no motion to grasp a rattle she is looking at. But then she subsequently brings to her mouth the rattle she has grasped independently of sight and sees the hand which holds the object, her visual attention results in immobilizing the movement of her hands; however, her mouth was already open to receive the rattle which is 1 cm away from her. Then Lucienne sucks the rattle, takes it out of her mouth, looks at it, sucks again, and so on. (Piaget 1953, pp. 102–103)

Piaget goes on to describe this as a new kind of schema within which infants can grasp what they see, and see what they grasp: a reciprocal relationship. For Lucienne, the object is no longer the thing of looking, nor the thing of grasping, but an entity existing in a more objective representation. Regardless of the reliability of Piaget's observations, his conception of a reciprocal schema shows us how two initially modality-specific (partial) representations of the environment (in this case, two unimodal schemas for acting on the rattle) can be enriched almost fortuitously by virtue of the spatial and temporal coincidence of the modalities. The resulting multisensory representation of the object, while still partial, is enriched and more objective since it goes beyond the immediate behavioural goal of either of the actions being performed.

If Mareschal et al.'s approach is to fully describe the nature of emergent cognitive abilities, then the multisensory constraints of the developing organism will certainly need further consideration. In particular, computational and robotic models of both modality-specific constraints (in neural machinery, and the interface of that machinery with the environment via the body) and also the constraints acting on the integration of these systems will help to further our understanding of how representations of the environment emerge.

Piaget's concept of a reciprocal schema prompts us to consider research demonstrating a gradual integration of action systems in early life, as this may point toward the development of mental representations or schemas that go beyond the simple satisfaction of an immediate goal. While much multisensory infancy research points toward the early unification of the senses enabling infants to detect a large array of amodal relations (Bahrick et al. 2004; Gibson 1969; Lewkowicz 2000; Phillips-Silver & Trainor 2005), research addressing crossmodal spatial orienting responses in infants appears to indicate a more prolonged period of integration (e.g., Bremner et al. 2008; Neil et al. 2006; von Hofsten 2004). It is possible that the gradual integration of such multisensory action systems may, by going beyond the immediate behavioural goals of initially separate unimodal schemas, enrich the representations that human infants acquire in the first months of life, and indeed determine the nature of cognition in adulthood.

Constructing minds: The development of mindreading abilities in typical and atypical trajectories

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Abstract: From our deep interest in the neuroconstructivist framework, we would like to comment on two fundamental aspects of Mareschal et al.'s work: the role of neuroconstructivism for clinical work with people suffering from developmental disorders; and the relation between the process of progressive specialization and the increasing abstraction of representations in development.

Mareschal et al. (2007a) consider two fundamental aims in the study of developmental disorders: "to identify appropriate methods of remediation" and "to use disorders to help our understanding of the normal processes of development" (p. 160). The authors broadly develop this second aim, showing that atypical development permits the study of developmental processes in situations with different constraints (even if assumptions must be cautious because atypical development is not necessarily a window to normal development: Karmiloff-Smith 1998b). However, they do not extend their first aim. We understand their work does not have a clinical orientation, but we consider the development of the implications of neuroconstructivism fundamental for the implementation of intervention programs aimed at improving psychological functioning in people with cognitive

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difficulties. Only by tracing the atypical trajectory of a process from the beginning is it possible to try and remediate cognitive deficits by emphasizing developmental strengths from as early as possible (even before behavioral deficits are evident).

Frequently, intervention is solely based on behavioral measures, without considering the possibility that a similar behavior may rely on different processes. In some cases, discovering these underlying processes should be the main objective of remediation because the generalization and adaptability of behavior may only be guaranteed if we use them as the basis for intervention. In our opinion neuroconstructivism's *radical rejection* of Marr's levels could be extended to the need to consider more than just the behavioral level in the design, implementation and evaluation of intervention programs.

In addition, neuroconstructivism's opposition to the maturational and modular approaches of development can be argued not only from its theoretical consequences, but also from its effect on clinical decisions, specifically on the futility of intervening in those domains that are considered preserved. For instance, Williams syndrome (WS)'s uneven cognitive profile may seem to support modular perspectives that describe preserved linguistic and social abilities and therefore, from these approaches, intervention in these domains is considered unnecessary. However, evidence has shown that language and social understanding abilities are far from intact in WS (Karmiloff-Smith et al.1997; Sotillo et al. 2007). Since diagnosis is obtained early on, it is essential to intervene in these and other areas as soon as possible.

In developmental disorders, atypical functioning of ontogenetic processes is expected. Mareschal et al. establish two driving forces in development: *proactivity* and *progressive specialization*. However, they say progressive specialization "*does not seem to be the whole story*" (p. 213; emphasis ours) because representations also go through a process of progressive abstraction. The "*tension*" authors find between the processes of specialization and explicitation is evident, but it is still necessary to explain their coherence, both within and between different functions.

One possibility is that each process has a different influence on diverse cognitive functions. Rivière (2003) proposes a Vygotskian based taxonomy of four initially hierarchical and cumulative psychological functions: F1 or modular unspecific (e.g., brightness perception), F2 or constructive nonsocial unspecific (e.g., object permanence), F3 or rudimentary-higher (e.g., language) and F4 or proper-high-functions (e.g., multiplication). Set on a continuum, F1 would be highly modular, associated with a precise neural localization, inflexible, and very efficient; while F4 would depend completely on culture and require explicit instruction. Development of F1 and F2 would lean fundamentally on specialization processes beginning as automatic in F1, and progressively becoming more dependent on experience in F2 and F3 (already being specifically human and dependant on social interaction). Development of each psychological function would rest differently on each developmental process, although both are necessary; and their coherence is particularly relevant in cognitive functions that imply redescription but also permit progressive specialization.

Representations specialize by getting more efficient and context dependent. However, context sometimes does not offer sufficient clues. It is not stable, and therefore explicit representations are also necessary for a systematic and compositional cognition. Implicit, embodied representations remain available when automatic, efficient functioning is required, but explicit representations permit independence from context, conscious reasoning and interrepresentational relations (Karmiloff-Smith 1992). Abstraction will be greater in higher functions, which require social interaction in such a way that explicitation needs not only internally but also externally generated social activity. F3 (as theory of mind –ToM) are just in the vertex of biology and culture, and allow approaching the role of *ensocialment*, *embrainment*, and *embodiment* in typical and atypical development.

People with WS are truly motivated to maintain social relationships and are rather capable of recognizing emotions. Nevertheless, from the assumption of an atypical developmental trajectory from the beginning at multiple levels, it does not seem viable to describe a preserved ToM module, or even submodule (Tager-Flusberg & Sullivan 2000). Instead an atypical trajectory in developmental processes is predictable.

The influence of specialization and explicitation on the development of ToM abilities in WS children has been analyzed in our lab (Campos, in preparation), and the results showed a lower performance in ToM than expected from their mental age. Furthermore, development of explicitation competences of mental states appeared particularly delayed in this group. Consistent with Karmiloff-Smith's (2006) predictions for atypical development, the processes of specialization and explicitation seem affected in WS in the social domain.

Research results are essential for intervention. If implicit processing abilities are better in WS, it is then possible to use an implicit approach in a clinical setting. Diverse developmental trajectories should imply different ways of remediation. Intervention with people with autism usually implies teaching some F3 as if they were F4, by explicit instruction (Howlin et al. 1999). However, in WS it could be more efficient to intervene based on their strong points: intersubjetivity and empathy, and to use their genuine interest to establish social relationships to provide them with social strategies for understanding mental states.

The neuroconstructivist perspective has an interesting potential, and we consider it crucial to extend its implications to clinical intervention, in order to improve the quality of life for people with developmental disorders. Research on optimal clinical strategies in different developmental situations will also have theoretical implications for the study of ontogenetic mechanisms. To achieve this, Rivière's taxonomy of functions could be a useful tool in that proactivity and progressive specialization would not need to be "the whole story," as they both would play their own part in every psychological function.

The concept of coregulation between neurobehavioral subsystems: The logic interplay between excitatory and inhibitory ends

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Abstract: *Neuroconstructivism, Vol. 1: How the Brain Constructs Cognition* implies that brain functioning depends on biofeedback and ecological trajectories. Using the building blocks of Boolean algebra known as logic gates and models of distributed control systems, I suggest that levels of regulatory states are responsible for optimal, pathological, and developmental processes. I include the impact of regulatory and nonregulatory functions on structural development.

Mareschal et al. (2007a) is a breakthrough in that it unifies many diverse approaches, each of which gives a partial explanation for brain functionality, into a more complete and modern interpretation. Building blocks of Boolean algebra known as logic gates and models of distributed control systems can serve as elucidation for levels of regulatory states that are responsible for optimal, pathological, and developmental processes as they

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manifest themselves in regulatory and nonregulatory functions to impact structural development.

The immediate implications are: (1) The complexity of feedback mechanisms between all the systems involved is more than earlier assumed, and (2) The optimal functioning of development is dependent on regulatory and nonregulatory states of the brain working within the body and the environment.

Regulation was defined earlier as the ability of the organism to return to baseline after mounting specific responses to an environmental stimulus. *Neurobehavioral coregulation* is defined as the capacity of the organism to subordinate all neurobehavioral capacities to enhance learning that allows it to be adaptive to the environmental requirements. It is also defined as the capacity of the organism to return to balance, following the adaptation of the enhanced neurobehavioral subsystem to the environmental stimulus. These processes support the successive maturation of all neurobehavioral subsystems, while working together and in competition with each other, towards a coordinated balance by increasing or decreasing responses to each other's state.

The importance of neurobehavioral function of regulation has been identified in several neurobehavioral MRI and EEG studies (e.g., the works of Als et al. 2004; Duffy et al. 1994; and Hofer 1994). The studies from our lab (Ferber & Makhoul 2004; 2008) show the interplay between the motor and the state/sleep/awake subsystems in full-term and in preterm infants (i.e., that the motor system activation is the source of inhibition of the attention system and vise versa).

As with a distributed control system, each subsystem output is used for regulating other subsystems. Thus the subsystems can be viewed as controllers or regulators that control one another. Each regulator can be viewed as comprising numerous logic gates.

A regulator within a distributed control system maintains an output in an optimal range. According to my view, the balanced control between the subsystems exists to avoid situations of extreme arousal or decline, as noted, for example, in situations of omnipotence versus helplessness or depression versus hypomania. A hyperalert condition of a subsystem that overrides the control of the other subsystems may lead to the decline of this subsystem, as observed, for example, in bipolar affective disorders.

Boolean algebra building blocks known as *logic gates* may be used to construct a model for explaining neural connectivity as well as neurobehavioral subsystems. A change in a state of a subsystem can be described as the product of an excitatory input and a NOT (inhibitory) input applied to an AND (excitatory) gate. If the excitatory input is active and the inhibitory input is not active, then the gate (subsystem) output will be active. Alternatively, if the inhibitory input is active, then the gate (subsystem) output will be not active regardless of the state of the excitatory input. However, we suggest that AND gates and NOT gates describe a function of deregulation in neurobehavioral subsystems. The same is true for an OR gate, in which the output is active if one or more of its inputs is active.

In contrast, an XOR gate which comprises 2 inputs, A and B, will have an active output if either A or B but not both are active. This could be an example for a regulated function of the neurobehavioral subsystems. See the truth table (Table 1) below:

Table 1 *(Ferber). Truth Table for XOR gate*

Input 'A'	Input 'B'	Output
Not Active (0)	Not Active (0)	regulated (0)
Active (1)	Not Active (0)	Active (1)
Not Active (0)	Active (1)	Active (1)
Active (1)	Active (1)	regulated (0)

The brain can be thought of as comprising a huge number of different types of the above mentioned basic logic gate types. Since there is a synaptic delay (the equivalent of propagation time delay in logic gates) in the operation between input activation and output change of state for every logic gate in a process, a relatively long execution time for every brain function might be expected. However, as in Boolean algebra, the rules for minimization of logic gates required to implement a logic function apply. By minimizing the number and complexity of the logic structure as above, the propagation delay time is decreased. The brain may be able to simplify complex logic functions and structures as above. This suggests the relatively minimal synaptic delay time for the complex cortical and subcortical interrelations (e.g., the impact of the limbic system and hypothalamus on the frontal control).

To explain discontinuity and nonlinear trends in development, *Neuroconstructivism* suggests a transition of observed behavior from one equilibrium state to another (see figure in Mareschal et al. 2007b, p.101, and the equation on p. 102).

Such developmental transitions are emphasized using a behavioral variable X as a function of parameter W. X grows up to a peak and then goes through a transition stage, characterized by instability and discontinuity, to another stable state which in turn grows to another peak and so on. This approach explains the macro picture of development through stages, each of which is a stable state, up to a transition point. It could also explain the interplay between the individual neural cell and its neural environment. Whenever an individual neuron is able to fire and is not regulated by other neurons, we have an unstable transition from one stable state to another. To answer one of the book's questions, I propose that the functional instability and nonregulated states may bring about structural changes which in turn are shown in developmental changes.

The brain works between peaks of arousal and decrement. Its efficient work is manifested in environmental conditions that support its interplay between peaks of neurobehavioral subsystems, up to a level of pleasure and harmony.

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Neuroconstructivism: Evidence for later maturation of prefrontally mediated executive functioning

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Abstract: The authors of this commentary concur with the viewpoint presented by Mareschal et al. (2007a; 2007b) concerning the relevance of neurological data when theorizing about cognitive development. However, we argue here that Mareschal et al. fail to consider adequately the relevance of reorganizational brain events occurring through adolescence and early adulthood, especially regarding the prefrontal cortex and the ontogeny of executive functioning. In addition, evidence from the lifespan neurodevelopmental literature indicates that increased activity of neural networks may signify less efficient processing. This observation is of potential relevance when considering the neurological changes associated with cognitive development during childhood and adolescence.

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Mareschal et al. present two well written volumes articulating their version of neuroconstructivism. Specifically, these authors seek to probe the mechanisms and processes whereby the inchoate infant develops cognitively and behaviourally into a sentient, cognizant adult. The authors advocate an integrative, multidisciplinary framework, incorporating data from a range of methodologies, including cognitive studies, computational modelling and neuroimaging.

The authors directly take issue with the Marrian view that levels of analysis can be considered independently at the computational, algorithmic, and implementation levels. Instead, they place much greater weight on the mutual constraints operating between levels of description. Specifically, the authors argue that theorizing about cognitive development should be explicitly informed by considerations of processes occurring at the neural implementation level – a view with which we firmly concur. However, Mareschal et al. apparently neglect to acknowledge the degree of neural rewiring that occurs at later stages of individual development. Specifically, there is accumulating evidence of significant reorganization of the neural substrate occurring during adolescence and even into early adulthood (Casey et al. 2000; Huttenlocher & Dabholkar 1997; Paus 2005; Spear 2000). These reorganizational processes take place during a phase of development when fundamental modular neurodevelopmental capacities such as those presented by Mareschal et al. (e.g., visual perception, habituation, phonological development, reading) have already been acquired (Luna et al. 2004). Potentially linked to these neural changes (and notwithstanding issues pertaining to adoption of the maturational versus interactive specialization position; see Foster 1997 for a related discussion), there is evidence of development during the teenage years with respect to elements of higher cognitive functioning, particularly regarding the ontogeny of executive functions (Luna & Sweeney 2004). Again, this is a domain of the extant literature that is apparently neglected by Mareschal et al. across the two volumes. It is of considerable interest to reflect on how the authors' conceptual framework would address these and related issues, which we are currently investigating empirically in Western Australia (via the Western Australian Pregnancy Cohort Study, evaluating a group of individuals who have been followed developmentally since before birth through to their current age of 16–18 years). Of potential relevance is the consideration that executive functions are not usually regarded as modular in either the weak or strong (i.e., Fodorian) theoretical sense.

In addition to the main conceptual issues discussed above, some more specific assertions made by the authors are also questionable with respect to the nexus between prefrontal cortex and executive functions. Of specific interest is the authors' contention (vol. 1, p. 65) that it is difficult to account for "decreases in the extent of cortical activation in terms of the progressive maturation of prefrontal cortical areas." This position is not justified by the authors with respect to independently acquired evidence or data, and it represents an interesting contrast regarding other areas of the lifespan developmental literature. For example, in the aging literature it has been argued that overactive cortical networks (as evidenced, for example, by functional neuroimaging investigations) are indicative of less efficient functional capacity, and that such overactivity may portend decline and dissolution of those networks and the cognitive functions they subserve (Dickerson et al. 2005; Hamalainen et al. 2007). It has been further suggested that, in older individuals, differences in regional brain integrity may be linked to functional reorganization through changes in processing strategy (Greenwood 2007). It seems plausible that a converse process may take place during acquisition of cognitive skills, as neural networks become more finely tuned and selective with respect to those external and internal environmental events that are necessary and sufficient for specific networks to be activated. In summarizing this section of text (vol. 1, p. 67) the authors contend that "frontal cortical regions, traditionally believed to be slow to mature, may be active from early in life." However, Mareschal et al. apparently omit to consider the degree to which such activation patterns may be modified across childhood and into early adulthood, specifically with respect to higher cognitive functions – as previously noted. Considering the multiple cytoarchitectonic regions comprising the frontal cortex (a disproportionately large and highly functionally elaborated brain region in humans relative to other mammalian and primate species), we think it is overly simplistic to adopt a uniform, homogeneous position with respect to the maturation of capacities subserved by this region (see Rabbitt 1997 for a review). Moreover, the authors themselves acknowledge (vol. 1, p. 213) that "cognitive development throughout late childhood and the teenage years is a story of increasing abstraction," and that with respect to the neural substrate underlying this process of increasing abstraction "one candidate may be the prefrontal cortex" (vol. 1, p. 214).

A new manifesto for child development research

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Abstract: This book is an excellent manifesto for future work in child development. It presents a multidisciplinary approach that clearly demonstrates the value of integrating modeling, neuroscience, and behavior to explore the mechanisms underlying development and to show how internal context-dependent representations arise and are modified during development. Its only major flaw is to have given short shrift to the study of the role of genetics on development.

Books like *Neuroconstructivism* (Mareschal et al. 2007a; 2007b) come along far too infrequently. This two-volume set is nothing short of a manifesto for how the study of child development in the twenty-first century should proceed.

The three most important chapters of Volume 1 are Chapters 1 (Introduction), 5 (Principles, mechanisms and processes) and 13 (Conclusions and challenges for the future). Taken together, these chapters alone can be viewed as a manifesto for how research in child development should proceed in the future. This book covers a wide range of interdisciplinary topics, with a particular emphasis on modeling, especially modeling of the connectionist kind.

The connectionist revolution came to psychology in the mid 1980s. The ideal starting point for connectionist models at that time was generally considered to be an undifferentiated (artificial) neural network substrate with few, if any, constraints that corresponded even remotely to what might be going on in an actual brain. But we must not forget that connectionism 20 years ago was still dueling with symbolic AI and that many of the early models, while necessary as proofs of the power of connectionism, were uninteresting from the standpoint of actually contributing to an understanding of the mechanisms underlying cognition. Now that those early battles are a thing of the past, connectionist models have gradually adopted a far more sensible middle ground in which modularity, and even rules, are acceptable, as long as they can be linked in some reasonably broad fashion to neural substrate. This book incorporates constraints from real brain functions into the connectionist models it describes, successfully integrating, insofar as possible, low-level neural constraints, brain-level constraints, and behavioral constraints.

To begin with, Mareschal et al.'s manifesto puts internal representations back at center stage in an attempt to understand

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not only how they drive cognition throughout the course of development, but how they emerge and are modified by both the "external" environment (i.e., embodiment) and the "internal" environment consisting of other regions of the brain (what they call "embrainment").

Representations have been somewhat out of fashion since the antirepresentational stances of Brooks (1990), Port & van Gelder (1995) and, especially important in the context of development, Smith & Thelen (1993) became popular. The authors of *Neuroconstructivism* seamlessly fold these more radical perspectives into their own via the notion *partial representations* and *proactivity*. To me, the authors' partial representations look for all the world like a retread of Hebb's notion of a cell assembly (Hebb 1949). (In perhaps the most surprising oversight of the entire book, the authors do not even cite Hebb's work, which is so intimately connected with their own in many ways.) They go on to summarize neuroconstructivist development (Ch. 5) as being "about how context-dependence is progressively expressed through partial representations" (p. 93). For someone who has spent more than 20 years preaching the gospel of flexible, context-dependent representations (specifically, in the area of analogy-making) that are gradually built-up by means of a continual interaction between high- and low-level constraints, these words were music to my ears. The authors propose three underlying domain-general and level-independent mechanisms that implement context-dependent representation-building – namely, cooperation, competition, and chronotopy (the "idea that there is a temporal order in the emergence of functional units") (p. 12). These cores ideas of neuroconstructivism are right on target.

The authors correctly reject Marr's (1982) tripartite division of cognitive levels of description. The independence of these levels was one of the cornerstone principles of traditional AI. The authors' unambiguous rejection of these ideas in favor of a view in which interaction between levels and with the environment is paramount for the emergence of the partial representations. They appeal, however, to parsimony as one of their reasons for rejecting Marr's views. This is a mystery to me. Parsimony may be fine as a guiding heuristic for physics, but it's a lousy one for cognition, simply because cognition came to us via the twists and turns and inability ever to back up that characterize evolution. And this is anything but parsimonious.

This then leads to perhaps the most serious criticism of this book: namely, that is has given short shrift to the role of evolution in general, and genetics in particular, in development. As a manifesto of how child development should be approached, I find it strange to see but a single page (pp. 218–19) devoted to genetics and development, and to find that the page concludes with, "... in humans, genes provide only very broad sorts of constraints on the representations that emerge in cortex" (p. 219). This statement borders on incomprehensible to me. That the interaction of genetics, environment, and behavior has profound and lasting effects on behavior and development is no longer open to serious debate. To cite a few examples, CREB genes certainly play a role in memory and recall, even if the exact mechanisms are not; BDNF genes affect visual development; FOX2P almost certainly has some role in enabling language, even if, once again, the details are still unclear. And the list grows longer by the day. And memory and recall, vision and language are without question crucial to the development of representations in the cortex. In other words, the message for future developmentalists should be: While you (almost certainly) don't have to go to the level of physics or quantum mechanics to explain cognitive development, you (equally certainly) can no longer be content to stop at the level of neurons. So, just as the authors rightly reject Marr's computationalism in which the implementational substrate was not supposed to matter to cognition, it seems equally valid to criticize their not including this important area in their vision of the way forward in developmental research. The closest the book comes to taking up some of these issues is in the chapter on atypical development. But a much fuller development of this is absolutely necessary.

There are other, more minor points that should be corrected in later editions of this work. The authors write, "... one of the most important conclusions from the formal study of learning is that *there is no such thing as an unbiased or unconstrained learner* ..., so cognitive development therefore reflects the outcome of constrained adaptation" (p. 20). These words could have come straight from Terry Regier's (1996) book on constrained connectionism, entitled *The human semantic potential;* and yet, this work is not even cited.

In conclusion, this is a first-rate book, a major contribution to the literature on development. I hope it will serve as a broad research manifesto on how interdisciplinary research in child development should be done in the upcoming years.

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Selectionistic neurocostructivism in evolution and development

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Abstract: *Neurocostructivism* aims to illustrate and explain cognitive development in relation to the underlying neural structures, with the help of computational models. This enterprise should be grounded both in the evolutionary and in the developmental perspectives. In both, selection plays a fundamental role in the construction of neural and cognitive structures.

Neuroconstructivism (Mareschal et al. 2007a) is an ambitious, brave, pioneering attempt to integrate system neuroscience and cognition across their current boundaries, within a developmental perspective. Computational modeling might be the best tool for such a complex task. This project is what we need if neuroscience has to have any future at all. I shall certainly go back to this book in the coming years, to refine my understanding of some of the rich, theoretical framework it explores.

I had some difficulties in grasping whether *constructivism* applies to the way cognition emerges from the brain (as in the subtitle), to how the brain and cognition codevelop, or to both. From a developmental point of view, I shall argue about the second interpretation. Let us go to facts. Accumulated evidence overwhelmingly demonstrates the generalized occurrence of exuberance and regression in brain development. Adult neural (and, I will argue, cognitive structures) emerge by selection from a richer (but constrained) juvenile stock. This applies not only to neuronal overproduction and death (as mentioned in ch. 2) but also to the generation of long axons, axonal branches, synapses, dendritic branches, number of spines, neurotransmitter receptors and/or expression, and so on. (reviewed in Innocenti & Price, 2005). In cognitive development the establishment of phonemic boundaries early in the postnatal period (Kuhl & Melzoff 1996), and the evidence of a progressively more restricted activation of neural structures during the acquisition of skills, documented by imaging and electrophysiological data are clear examples of selectionism, as well as, I believe, Johnson's concept of "interactive specialization" (Mareschal 2007a).

The authors make only weak attempts (p. 7) to resolve the apparent opposition between selectionism and constructivism. I feel this dyad lies at the core of understanding how genes

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and environment (via neural activity) interact in evolution and in development. The opposition between selectionism and constructivism can be overcome by precise reference to the time-frames considered. In evolution, the power of selection is unchallenged and two-sided. One side is the selection of the genetic networks responsible for the harmonious emergence of brains/bodies and cognitions/behaviors most appropriate to the ecological constrains of a given environment ("context" in the book). The second is the selection of permissive developmental algorythms, in particular development by exuberance and regression of neurons, axons and so forth, mentioned above, which allows crossed adjustments of brain structures (e.g., Kingsbury et al. 2002), bodies, cognitions, and behaviors, and which actually allows evolution itself (Innocenti 2006). Now consider the developmental time-frame. Evolutionarily selected neural and/or cognitive structures are validated by experience in a context-dependent manner. Competition, cooperation, and *chronotopy*, which the authors identified as general developmental mechanisms, become relevant. Active exploration (experimenting or proactivity) is the expression of the evolutionary heritage, which, at the cognitive level might well consist of "partial representations" to be tested for their relevance in the real world. Only part of the structures selected in evolution survives this second wave of selection. Most important, they will not be tested and selected simultaneously, thus providing the framework for construction by sequential selections, a scenario we proposed for the development of axonal arbors (Zufferey et al. 1999).

I loved the concept of *partial representations* proposed by authors, although *representations* seem difficult to define rigorously (pp. 4 and 5) and to test experimentally (pp. 221–22). Several questions spring to mind, for example.: How complex is a representation? Is it reducible to elemental parts? How far? In any case, partial representations seem to be economical in terms of neural resources and are open to completion by developmental experience and/or learning, in adult life.

In conclusion, I feel that one should accept the overwhelming evidence that environment and activity, in development are sculpting-out brain, body, cognition and behavior by selection, within the boundaries established, for each species, by evolution. Some further elaboration of the evolutionary heritage may occur based on cycles of generation, testing and validation/rejection of elemental structures were they axonal branches, synapses or representations. I would prefer to call the whole process *selectionistic neurocostrutivism.* The opposition then is not so much between selectionism and constructivism as between permissive and instructive morphogenetic factors, including experience. I have struggled with some of the concepts before, although not to my full satisfaction (Zufferey et al. 1999).

One crucial question is, what happens when "context," in development, fails to validate the neural and/or cognitive structures that evolution has selected. This is equivalent to asking whether the information provided by environment is permissive or instructive. Many examples of abnormal development are specified in the book all of which illustrate genetic abnormalities (Table 11.1, p. 164). Examples of abnormal experience in early development due purely to environmental factors, such as sensory or social deprivation (reviewed in Innocenti 2007), toxic insults (e.g., fetal alcohol syndrome), thyroid disturbances (Berbel et al. 2007), and others, may be more informative. Some of them illustrate the response of the developing organism to the abnormal, and therefore potentially instructive, environmental conditions. The evidence for an instructive role of development is slim. Often the outcomes are nothing more than arrested development with no adaptive consequences whatsoever, providing strong evidence that development is rather tightly constrained. Thus, if the environmental conditions which drive selection in evolution are not met, the evolutionary heritage is deleted. This recalls Wiesel's statement that: "Innate mechanisms endow the visual system with highly specific connections but visual experience early in life is necessary for their maintenance and full development" (Wiesel 1982).

This book is a very stimulating achievement. Its organization in Part 1, Foundations, explicating the main principles and the reasons for attempting the great synthesis of system neuroscience with cognition and development; the Case Studies section demonstrating how the principles can be applied; and the final section, Conclusions, specifying at least some of the open issues and the future directions is excellent. The "Boxes" provide essential information for readers not familiar with the territories explored and are particularly useful for a broad readership. The book provides a solid attempt to establishing a new field of intellectual and experimental investigations which will hopefully grow in the coming years.

Beyond mechanism and constructivism

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Abstract: Neuroconstructivism is a hybrid of two incompatible philosophical traditions: a radical idealism insisting upon the free activity of the Subject; and a radical materialistic anthropomorphism, which ascribes inherent properties of humans (e.g., the ability to construct) to nonhuman objects or body parts (e.g., the brain). The two traditions can be combined only by obscuring or confusing the basic notions.

Long ago, idealist philosophy taught about the Subject, which actively constructs the world of objects, as a product of its own externalizing action. Can this activist view be integrated into the context of modern neuroscience?

Neuroconstructivism (Mareschal et al. 2007a) is an example demonstrating that the we cannot simply take the features previously belonging to the mind and reattribute them to the brain, leaving the rest unchanged. The authors' brave attempt to integrate different approaches is laudable. However, the intended synthesis came at the price of making the fundamental concepts so vague and fuzzy that they can be filled by any deliberate content. Let us follow the tragic fate of three of these concepts.

Representation is the central concept. "Cognitive development is about how representations emerge" (p. 89). But what is representation? If there is anything common in the plethora of definitions of this polysemous word, it is that a *representation* presumes three things: one that is represented; one that represents; and one to which (dative case) it is represented. For Catholics, for example, the Pope represents Jesus during the temporary absence of the latter; note that if there are no Catholics, the representational function of the Pope would not have any sense. An ambassador represents his state in a foreign state. My attorney can represent me in the court.

But to whom, or for whom, do mental representations represent the world? To the spectators in the theater in my head? Mostly, representations are described with the adjective "internal," obviously meaning that they are contained within something. (See Järvilehto 2001 for the usage of inner/outer relationships.) What might this container be? Sometimes it appears to be the brain (e.g., pp. 71, 147), sometimes the mind (p. 16); representations can exist "in the brain, body, and environment" (p. 100). Finally, a representation is "any component . . . if it can have an independent effect on behavior" (p. 100), a definition which is practically identical to the assertion radically

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rejected by the authors, that there is no representation (Thelen & Smith, 1994). In a symptomatic footnote, the authors confess that they "... remain agnostic as to where exactly mental representations lie ... between brain states and world states" (p. 28). This is in complete agreement with the classical idealistic dichotomy between subject and object (here: the brain and the world).

If we say that "stimuli do become represented by individual neurons" (p. 112), we simply mean that these neurons fire with a much higher rate to some stimuli than to others. What does the term *represent* add to this fact? If a drop of water does not leave a trace on a mineral, but a drop of an acid does, then, does the mineral represent the acid?

In their notion of partial representations, the authors take a big step toward the concept of representations as "functional systems" (Anokhin 1974), as anticipatory interactions between the organism and its environment (Bickhard 2005), but they were probably afraid of their own courage and thus stopped halfway. The term *partial* is misleading because it insinuates the possibility of something like full representation. Is it a representation of an object in all its details including all features of all its elementary particles, even those not yet discovered? The authors' answer is very simple: "the most accurate and complete representation ... will be provided by the raw sensory data" (p. 112). Therefore, to get the most complete representation of stars, we should not attend lectures in astronomy but merely record all retinal cell activity while we are looking at the sky. This idea is a logical consequence of the authors' general view of cognition as constraint, as filtering and processing of information rather than obtaining it. Within this view, indeed, cognition can only impoverish raw data.

Constructivism. This is the notion that gives its name to the whole approach. If constructivism is minimally defined as a credit for proactive features of behavior, then I am a constructivist too. But the proactivity rightly emphasized by the authors is not construction, because the cognitive organization is actively extracted from the world, rather than being imposed by the subject (Newspeak: brain). Likewise, activity is not just the ability to filter out the irrelevant and facilitate the processing of relevant information. The organism does not filter information but picks it up according to its needs and tasks, as "a datum for a certain hypothesis will not only sensitize and bias an intelligence officer toward the incidental flow of information which is indicative of the same hypothesis, but will ... also lead the officer to seek such information." (Navon 1981, p. 5).

The two main mechanisms of the constructivism, cooperation and competition, simply describe positive and negative effects, respectively, of any element A on an element B. They are not principles found out in an empirical study of development (as the presence of right angles is not an empirical feature of squares), but just consequences of our use of words "element," "effect," and so on.

A legitimate way to describe a hard-to-define approach is to use definitions of its rejected alternatives. Thus neuroconstructivism rejects "... that cognition unfolds according to some predestined blueprint encoded in the genes" (p. 87), that the child is "a passive organism imprinting on environmental events over which it has no effect" (p. 96), "the same way that a sponge would soak up water" (p. 214), that perception is "... a purely serial, feedforward sequence of processing stages" (p. 109). Does somebody believe in such things? What is the value of a triumph over this army of straw men?

Embodiment. It is true that "talk of embodiment ... has become increasingly frequent in mainstream psychology" (p. 74). Unfortunately, however, the ideas usually become mainstream talk when they lose their essence. The authors define embodiment as a constraint. My cognitive activity takes into account the fact that I have only two arms. "... an agent is embedded within a body that serves to constrain the agent's interactions with the environment" (p. 49); "each brain region develops within the context of other parts of the brain" "just as the brain is situated within a body" (p. 59).

This conception of embrainment and embodiment would readily be embraced even by spiritualists. Of course, in the conditions of a finite human life, the agency of the immortal soul is constrained by the peculiar constitution of the earthly body. The authors miss the fact that embodiment is not just placing "the agent" (fig-leaf for "the subject") into a human body, and the latter into a cultural environment, as their Fig, 4.1e (p. 72) suggests. The very existence, emergence, and development of "the agent" is impossible without this body and this environment; they are not constraints but sources and causal factors, condiciones sine quibus non a human. Conceiving of embodiment as just a constraint is like conceiving of Christianity as regular attendance of Sunday services.

As Jordan (2000) formulated it, living systems do not possess knowledge; they *are* knowledge (see also Maturana & Varela 1980). We need not be prisoners of the wrong opposition: either passivity or constructivism. Cognition is not constructed by the brain using blocks of representations as a wall is constructed by masons using blocks of concrete. Cognition is a high-level energetic nonequilibrium within an organism/environment system, whose one component (the organism) must perform continuous anticipatory control of its behavior to maintain its stability. The brain plays a key role in this control, but it is not a creator of cognition, any more than the "mind" of old authors. Though it is true that the enormous complexity of the working brain can fascinate us, as the enormous power of the sun fascinated earlier people, future generations will smile at our modern cerebral cult like we now smile at the solar cult of our forefathers.

Representing development: models, meaning, and the challenge of complexity

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Abstract: *Neuroconstructivism* (Mareschal et al. 2007a) provides a useful framework for how to integrate research from different levels of analysis to model the multidimensional dynamics of development. However, the authors overlook the topic of *meaning*, a fundamental feature of cognition and subjective experience and also downplay the nonlinear nature of developmental causality. *Neuroconstructivism* is overly optimistic on the point of how well current computational models can address the challenge of complexity in developmental science.

Philosophers of science point out that good models should suggest experiments, allow predictions about the consequences of interventions or manipulations, and prompt new questions or directions for further research (e.g., Keller 2002). In this light, *Neuroconstuctivism* is a significant step forward in the use of modeling within developmental science. Particularly noteworthy, the authors have provided a conceptual framework that takes seriously the notion that the minimal unit of analysis necessary for understanding behavior and cognition is the "brain in a body in an environment" system (Chiel & Beer 1997; Nelson 2007). Although the argument against the usefulness of radical reductionism has been made by a number of developmentalists in recent years, it is certainly the case that many neuroscientists and psychologists continue to speak as if understanding the brain will yield a full understanding of behavioral and cognitive development. *Neuroconstructivism* provides a cogent argument against this reductionistic view and outlines a well articulated example of how to integrate research from cognitive studies, computational modeling, neuroimaging, and developmental psychology to model some of the complexities and

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multidimensional dynamics of the developmental process. I am in agreement with the spirit of this integrative effort, particularly its emphasis on context dependence, multilevel isomorphism, and developmental trajectory, and its acknowledgment that explanations of cognitive development must be consistent with our knowledge of developmental and evolutionary biology (Lickliter & Honeycutt 2003). However, I have several reservations about the scope of the present version of the neuroconstructive approach. These include (1) that the authors have downplayed the nonlinear causality often at play in the developmental process, and (2) have effectively ignored the importance of value and meaning in the formation and maintenance of cognitive representations.

It is surprising that a framework designed to address the development of cognitive representations, based on the assumption that "cognition is essentially a process involving the manipulation of information" (p. 208), effectively sidesteps the topic of meaning and the issue of subjective experience. Value and meaning must be addressed in any theory of cognitive development; information takes form only when it is personally meaningful. As recently reviewed by Tucker (2007), the formation of cognitive representations is achieved by the same limbic networks that provide the motivational control of behavior. In other words, the expectancies that guide cognition are personal and motivated. *Neuroconsructivism* does not adequately address the importance of meaning or the related issue of subjectivity, despite its emphasis on the "proactive" nature of development. This is an obvious shortcoming of the current framework and a significant challenge to computational modeling. In this light, the omission of reference to the work of Walter Freeman, which provides an important foundation for thinking about and modeling the links between meaning and representation, is surprising. As Freeman (2001) has pointed out, meaning derives from the entire brain and body, with the history of the organism built into muscles, endocrine glands, and neural connections. The chapter by Sporns (2007) that appears in the companion volume does provide an initial step in addressing the psychobiology of meaning by emphasizing the importance of value systems in neuromodulation and learning. The scope and application of the neuroconstructive approach would benefit from additional efforts focused on how to incorporate the role of value and meaning into its models of cognitive development.

With regard to the larger issue of modeling the developmental process, while development can sometimes be viewed as a chain of cause/effect relationships (a common assumption in computational simulations), these chains often turn out to be loops, where cause becomes consequence and consequence becomes cause. Indeed, this nonlinear and distributed nature of causality is a fundamental feature of the developmental process (Gottlieb 1997; Gottlieb & Halpern 2002) and the authors have not gone far enough in coming to terms with how to address this aspect of developmental complexity. Although *Neuroconstuctivism* does make a strong case for refocusing our attention from making simple causal attributions (to the genes or to the environment, for example), it does not provide a clear road map for how to model the varied systematic processes and interactions that take place within and between levels (i.e., genes, neurons, hormones, social interaction, culture) of the human developmental system (Johnston & Edwards 2002). Recent evidence from the rapidly growing field of epigenetics demonstrating the intricate regulatory networks of genes, their products, and the features of the organism's internal and external environment highlights the mind-boggling combinatorial complexity of the bidirectional traffic inherent in the process of development.

In sum, I found the authors overly optimistic as regards how far connectionist models of development will get us. Early in the text, the authors state their aim in *Neuroconstructivism* is to "explain development." This is an ambitious goal, to say the least, given that the process of development is a dizzyingly complex multidetermined phenomenon and the number of variables, interactions, and contingencies involved in the journey from fertilized egg to functional adult may well put its full understanding beyond human comprehension. This is not due to a lack of trying – thousands of scientists have worked on or are working on various aspects of this challenge. Keller (2002) has recently argued that there are likely some phenomena in the natural world that extend beyond our grasp, too complex to fit neatly into any of our models, theories, or explanations. The process of development may well turn out to be one of these phenomena. That said, it is also the case that a better understanding of the ways and means of development can make a significant contribution to how we understand nature and ultimately, how we understand ourselves. Despite its shortcomings, *Neuroconstuctivism* is a step forward on this quest. While it does not succeed in explaining development, it does succeed in providing an integrative model of the development of cognition that will likely suggest experiments, allow predictions about the consequences of interventions, and prompt new questions for research. That seems plenty to expect of this or any other functional model of development.

It's high time: Cognitive neuroscience lives

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Abstract: *Neuroconstructivism* (Mareschal et al. 2007a) heralds a departure from the standard "associationism" that has dominated the English speaking cognitive and neuroscience community for generations. Its central concept is context dependency: encellment, embrainment, embodiment and ensocioment. This reviewer welcomes the breath of fresh air in overcoming the "deconstructions" of postmodernism. The program is carried out with a carefully selected sample of empirical evidence with an emphasis on development. This review points to some of the books' strengths and shortcomings, and adds a few observations that carry the program further.

The English speaking scientific and philosophical communities have been dominated by Humean associationism: empirical observations are stuck together to compose explanations of observations at a higher order. In brain science this approach dates from Viennese neurology of the latter part of the nineteenth century: sensory inputs become associated in "association areas of the cortex."

Neuroconstructivism presents a different panorama. They see constructivist development as a progressive increase in the complexity of representations that is realized in the brain by a progressive elaboration of cortical structures. Interestingly, leads to 'cleverer' and not simply more knowledgeable organisms.

The authors describe this process as encellment, embrainment, embodiment, and ensociomentand give good reasons why each of these processes is necessary to provide a reasonably good understanding of the whole constructivist endeavor.

Without detracting from the enterprise as a whole, I do have some queries:

1. The authors' approach deals with complexity; why do they not explicitly say more about complexity theory, non-linear dynamics as it applies to one or another scales of investigation? (The exception is Chapter 5 written about a model by another author). They come close: They compare our world of artifacts, texts, media and cultural practices to the activity created *whorls* that form the "umwelt" of the blue fin tuna. Whorls serve as attractors in nonlinear dynamics. In the language of complexity theory, cultural practices when embrained through embodiment, serve as attractors.

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2. Why do the authors limit themselves to neurons and circuits in their chapter on embrainment and, despite the acknowledgement that populations of cells not single cells are involved in processing, ignore processes occurring in the fine fiber structures of dendrites, and axonal branching where the populations interact? Again they come close: in their chapter on principles, mechanisms and processes they note that the emergent functionality of the individual neuron depends largely on the chemical and cellular context of the neuron. In short, the fine fiber, ephaptic, and synaptic processes (and even glia) are more important for progressive development and cognitive processing than the brain's neuronal circuitry. Though the authors do not recognize this, connectionist models actually deal mathematically with neuronodes that represent connections among neurons, connections occurring in the fine fibers of the brain, not neurons per se. This is because most modelers erroneously describe the nodes as neurons.

A few specific embellishments: In discussing Piaget and his contributions, the authors point out that there is a failure in his contributions to deal with the dynamics that move the child from one cognitive level to the next. Both Piaget and I wrote for years about equilibration, a static reaching of equilibrium. But for both of us this view changed with the advent of Prigogine's "temporary stabilities far from equilibrium" (Prigogine 1980; Prigogine & Stengers 1984). Piaget, Inhelder, and I discussed this issue and agreed that stabilization in the sense of temporary stabilities was a required necessary improvement over our earlier views. Again, it is important to make complexity theory, stabilities as attractors, explicit in *Neuroconstructivism*.

In the treatment of vision some weaknesses become evident. The authors are struggling to release themselves from current interpretations of the results of experiments. The authors correctly criticize the way in which the so-called dorsal and ventral visual pathways have been exploited: that often the pathways are activated in reverse (as there are just as many connections in the reverse direction – as I have also emphasized (Pribram 1974). They do not go the distance, however, to suggest that object constancy can precede the divergence of the two as suggested by the results of (Zeki 1983; Ungerleider et al. 1977).

Furthermore, the elimination of cortico-cortical and subcortical thalamic connections that presumably underlie the ventral pathway does not disturb visual processing, while when the relevant subcortical to cortical pathways are disrupted, visual processing by the inferotemporal cortex ceases. All of this evidence provides additional support for the conclusions arrived at by the authors in *Neuroconstructivism* (Pribram 1986).

A last point about vision: In the second volume Chapter 2 is based on an isomorphic model of processing images in the primary visual pathway while Chapter 3 deals with processing in the same pathway in the spectral domain. The two points of departure are a matter of scale (gross vs. micro) but, as the two ways of dealing with imaging are very different, the differences should not be glossed over but addressed somewhere in the volume.

A final comment: The neuroconstructivist view predicts that representations will become progressively more fragmentary because they emerge within (and build on) increasingly complex representational contexts. In short, the representations are content, not location addressable. But retrieval codes are location addressable, thus there is some gross "localization of function" in brain systems.

In conclusion: *Neuroconstructivism* is, to my mind, a landmark contribution. I liked especially the treatment of habituation – and would add the amygdala and other basal ganglia systems to the discussion (see Pribram 2006). Also, the treatment of phonological development is seminal –[and I want to emphasize that the "motor cortex" in general – not only in audition – deals, *not* with the programming of movements, but with processing "targets" or "images of achievement" (see Pribram 1991).

As the reader can see, I am enthusiastic about the presentation that carries forward a program consonant with one that I envisaged (Pribram 1965) to which the authors have already added much. Just what the journal *Behavioral and Brain Science* is so good at stimulating.

Toward automatic constructive learning

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Abstract: Neuroconstructivist modeling can be usefully extended with algorithms that build their own topology and recruit existing knowledge, effectively constructing a hierarchy of network modules. Possible benefits include allowing abilities to emerge naturally, in a way that affords objective study, deeper insights, and more rapid progress, and provides more serious consideration of the implications of constructivism.

The authors (Mareschal et al. 2007a) make a convincing case that constraints from brain, body and environment should be taken seriously when trying to explain psychological development and that computational modeling has an important theoretical role to play in such explanations. My commentary focuses on some interesting comments made in *Neuroconstructivism*'s Box 1.1 (p. 13) concerning constructivist approaches to the modeling of development. There they raise the possibility that neural networks could mimic constructivist development with a hierarchy of networks such that the outputs of networks solving simple problems could serve as inputs to networks solving more complex problems. In this way, later and more complex knowledge could be based on, and benefit from, earlier and simpler knowledge.

Currently, most such models are designed and arranged by hand, where each network is trained separately and then combined in a designed hierarchy. The influential model of object processing featured in chapter 9 of Volume 1 is a good example of this approach (Mareschal et al. 1999). That model neatly explains the well-known décalage in development of object permanence between looking and reaching measures (Baillargeon 1987) by noting that information processed by ventral and dorsal visual streams needs to be integrated in reaching tasks, but not in looking tasks, which can rely solely on the dorsal stream.

One limitation of such models is that much of their ability is supplied by the human modelers who cleverly arrange the training and connectivity between various network modules. In this case, one network module learns to recognize objects based on their static features while another learns to follow the trajectory of moving objects. A third network module learns to reach for objects by integrating these two skills, thus explaining why successful reaching takes longer to achieve than successful looking.

Recent work in knowledge-based neural learning raises the possibility that the design and arrangement of such hierarchical networks could be done automatically by the learning algorithm itself without human intervention (Shultz & Rivest 2001; Shultz et al. 2007b). The algorithm used in this work has been dubbed knowledge-based cascade-correlation (KBCC) because it extends the earlier cascade-correlation (CC) algorithm to enable the recruitment of old networks into new learning. CC is a constructive neural learner (Fahlman & Lebiere 1990) that has been used to model a wide range of developmental phenomena (Shultz 2003). It works by starting with a simple network with

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only input and output units, and then recruiting single hidden units as needed to reduce network error. An interesting variant called sibling-descendant CC (SDCC) allows classic descendant candidate units to compete with sibling candidate units (Baluja & Fahlman 1994). As in ordinary CC, the candidate hidden unit whose activation correlates best with network error is the one that actually gets recruited. A descendant recruit is installed on its own layer just beyond any existing hidden units, whereas a sibling recruit is installed on the current highest layer of hidden units. Evidence indicates that SDCC produces equivalent coverage of developmental phenomena to that provided by classic CC, but with a greater variety of network topologies, most with less network depth and fewer connection weights (Shultz et al. 2007a).

KBCC is a natural extension of CC in which previously learned networks are saved and made available to be recruited in new learning. These older networks compete with each other and with single-unit candidates in the usual fashion. Namely, the candidate whose activations correlate best with network error is the new recruit. KBCC was designed (Shultz & Rivest 2001) to capture the pervasive tendency of humans to build their new learning on their existing knowledge rather than learning everything from scratch (Heit 1994; Pazzani 1991; Wisniewski 1995). Such knowledge-based constructivism can account for some of the ease and speed of human learning and for the interference effects that sometimes arise.

Prospects for simulating cognitive developmental phenomena with KBCC are good but only just beginning. A preliminary KBCC model of the benchmark balance-scale task (Shultz et al. 2007b) suggests that KBCC could cover a genuine torque rule, as opposed to a mere addition rule (Quinlan et al. 2007) in a terminal stage in accord with the likelihood that adolescents acquire such a torque rule by direct instruction in science classes (Siegler & Klahr 1982). Symbolic rules, such as the torque rule, which predicts that the side of the scale with higher torque (product of weight and distance from the fulcrum) will be the side that descends, can be inserted into the recruitment pool of KBCC in a neural form.

Although most KBCC simulations report faster and more accurate learning by virtue of recruiting existing knowledge (Shultz et al. 2007b), one simulation demonstrates that prior knowledge can be not just helpful, but even essential, in learning. That project shows that prior knowledge of divisibility is required for networks to learn how to detect prime numbers from examples of prime and composite integers (Egri & Shultz 2006).

The import of knowledge-based learning for modeling neuroconstructivism is that automatic organization of hierarchical, modular networks may now be within our grasp. Just as classic CC networks are able to construct their own topology automatically as they learn, KBCC can organize multiple networks into a hierarchy that allows the output of some older, knowledgeable networks to feed inputs of other units and networks and the outputs involved in new learning.

Letting computational models do their own thing seems preferable because it makes the modeling enterprise less artistic and more scientific. It allows the intelligence of computational systems to be taken out of the hands of skillful modelers and placed inside the algorithms themselves. In turn, this allows intelligent behavior to emerge in a more natural fashion, as opposed to being engineered by human handlers, thus affording a deeper glimpse into the way phenomena might really work. Models allowing such emergence may well be ultimately wrong, as virtually all models and theories are, but at least their workings can be more fully examined and tested in an objective, scientific manner, thus advancing the field more directly and more rapidly. In short, emergent models take constructivism more seriously.

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Authors' Response

Studying development in the 21st Century

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Abstract: In this response, we consider four main issues arising from the commentaries to the target article. These include further details of the theory of interactive specialization, the relationship between neuroconstructivism and selectionism, the implications of neuroconstructivism for the notion of representation, and the role of genetics in theories of development. We conclude by stressing the importance of multidisciplinary approaches in the future study of cognitive development and by identifying the directions in which neuroconstructivism can expand in the Twenty-first Century.

R1. Introduction

We are grateful to the commentators for highlighting many of the key ideas that lie at the heart of the neuroconstructivist framework. Among those key ideas are the following (see, e.g., **Bateson**, **Bremner & Spence**, **French**, **Innocenti**, **Lickliter**, **Pribram**):

1. Neuroconstructivism seeks to integrate research from different levels of analysis to model the multidimensional dynamics of development, including findings from cognitive studies, computational modeling, neuroimaging, and developmental and evolutionary biology;

2. Neuroconstructivism lays particular emphasis on the concepts of emergent specialization, context dependence, multilevel isomorphism (consistency between levels of description without reductionism) and developmental trajectories; and

3. Neuroconstructivism appeals to three domain-general and level-independent mechanisms to implement the building of context-dependent representations: cooperation, competition, and chronotopy (the idea that there is a temporal order in the emergence of functional units).

In articulating the neuroconstructivist framework, our aim in the two volumes was (as **Bateson** nicely puts it) to offer a road map to render usable long-held intuitions about the interplay between the developing organism and its environment. We believed the time was ripe for

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this endeavor because of the emergence of new methods for study the process of development in genetics, biology, brain imaging, and computer science.

We group our response to the commentaries under several headings. We begin by considering the theory of interactive specialization in greater detail. We then consider the potential tension that exists between neuroconstructivism and selectionism. In the next section, we address a cluster of issues involving the idea of representation: the relation between partial and full representations; how representations may become more specialized to domains across development, yet the system as a whole can demonstrate increases in abstraction, flexibility, and in some cases, context independence. Following that, we address the role of genetics in development, reconciling our belief in the importance of genetics with its relatively low profile in the two volumes. This leads us to consider two directions to extend the neuroconstructivist framework: to incorporate lifespan and evolutionary perspectives. We then address a set of individual issues covering chronotopy, developmental disorders, subjectivity and value, and the use of formal methods. We finish by acknowledging and rectifying some omissions, and consider the challenges facing neuroconstructivism in the future.

R2. Advances in interactive specialization

Innocenti and **Anderson** both make specific comments about processes related to the Interactive Specialization model (Johnson 2000; 2001) presented within our discussion of embrainment. Anderson presents a method for establishing the degree of unique specialization of cortical regions, defined as a cortical region that is involved in performing some computations but not others. In particular, he argues for a distinction between *computational specialization* and *domain specialization*. In computational specialization, regions develop increasingly well-defined subfunctional roles within an activated network; with respect to cognitive domains, specialization would be a property of the particular *network* of regions. In domain specialization, it is the *regions themselves* that become increasingly dedicated to a narrow range of cognitive functions, thereby restricting their involvement in other domains. Anderson then presents initial findings from a meta-analysis of functional magnetic resonance imaging (fMRI) studies and argues that they provide support for the computational specialization view: The unit of domain specialization appears to be the network of regions rather than regions per se.

While we have not defined the end-state of Interactive Specialization in the level of detail described by **Anderson,** we agree with his conclusions that the results of specialization may be cortical regions that play multiple roles in different domains. Each region has an increasingly specialized role as part of the network activated to support the computations necessary for a given domain. Indeed, this notion resonates well with the general idea of partial representations. However, developmental work argues that active brain areas move from broad and fuzzy, to less broad and more specialized (e.g., Durston et al. 2006). Such a shift would seem to indicate that regions lose at least some of their contribution to specific cognitive functions across development.

Anderson's approach is simple but powerful and offers provocative results. Of course, there are limitations to what a meta-analysis can achieve, imposed in the main by the quality and consistency of the contributing studies. The practical limitations of fMRI studies include the predominant reliance on subtraction methodologies, the poor temporal acuity, the mix of whole-brain analyses and region of interest analyses, and the variability of techniques employed within the analyses themselves (smoothing functions, thresholds, etc.). Some of the apparent involvement of multiple cortical areas in multiple tasks may be a consequence of the limitations of (some of) the studies included in the meta-analysis.

In our own work, we have embraced the distinction that **Anderson** has identified, and designed fMRI paradigms to test it empirically. The most important requirement, here, is that the cortical areas activated by different tasks should be evaluated *within the same participant;* otherwise between-participant variability may be mistaken for distributed processing. That is, if a region performs function x in one participant but function y in another participant, one might (mistakenly) infer that this region performs both function x and function y in the normal human brain. In the lab of one of our authors (M.S.C.T.), one current study employs multiple tasks within the broader domain of language (auditory comprehension, reading, naming, semantic retrieval, and gesture production) carried out by the same participants. The analyses target four regions of interest to examine their relative involvement in the functional networks activated during each task. The design is event-related to allow for analyses of functional connectivity between the regions; and the study uses a lifespan design with a cross-sectional sample from children of 7 years old up to adults of 75, to explore whether regional or network specialization alters with development and/or aging. The practical limitations of a paradigm such as this for addressing interactive specialization are that many of the interesting developmental processes will have been (largely) completed by the youngest ages in which it is practical to run the paradigm; and even with an event-related design, the temporal acuity can offer only a very blurred view of the computational relations between the regions involved. fMRI designs must therefore be complemented by methods that are more readily applicable to infancy and that offer better temporal acuity, such as electrophysiology (see, e.g., De Haan 2007; Nelson & Monk 2001).

Additionally, we suspect there is further progress to be made in exploring interactive specialization through computational modeling. Within this discipline, one must precisely specify what it would mean for emergent specialization to be (in the main) a property of networks of regions, with each region participating in many such networks. What exactly is the computational role of a region in these networks? Does the region offer, for example, modality-specific partial representations (e.g., dimensions of visual information)? Or a particular computational primitive (e.g., inhibitory control, analysis of sequences)? Or is it a chameleon, adopting different computational guises in each functional network? For ease of explanation, we would probably prefer the first or second options to be

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true. However, even simple connectionist networks can learn to demonstrate the third property.[1] Such "context sensitive" computations are intrinsic to connectionist networks, which is why we believe they are an excellent tool to investigate cognition within a neuroconstructivist framework. The key issue would then become to understand how such chameleonlike computational properties are exploited by, and change over, development.

R3. Neuroconstructivism versus selectionism

Innocenti argues that selectionism, the process of pruning neural connections to cull those that are irrelevant, noisy, or redundant, may provide a basis for Interactive Specialization. We agree wholeheartedly, with the caveat that constructive neural processes may also play an important role. It is worth making clear the perceived tension between constructivism and selectionism, before indicating why we think the two are in fact largely consistent with each other. Constructivist development argues for a progressive increase in the complexity of representations, which enables new competences to develop based on earlier, simpler ones. Within neuroconstructivism, this increase in representational complexity is realized in the brain by a progressive elaboration of functional cortical structures. By contrast, Innocenti points to the large accumulation of empirical evidence for the generalized occurrence of exuberance and regression in brain development. Under the selectionist view "adult neural (and . . . cognitive structures) emerge by selection from a richer (but constrained) juvenile stock" as Innocenti puts it. On the one hand we have elaboration while on the other we have regression.

We believe these positions are consistent if one views the exuberance and regression in terms of (potential) computational resources, and the elaboration of structures in terms of actual functions. For us, selection is an outcome of the fundamental processes of cooperation and competition that lead to the emergence of partial representations. **Innocenti** seems agnostic as far as how goal-directed the exuberance preceding the regression is, but a fair amount is now known about the experience-dependent, goal-directed elaboration of neural structures (see, e.g., Quartz & Sejnowski 1997). From a constructivist viewpoint, there is also a sense in which the emergence of partial representations in different regions sets the stage for the emergence of specialized networks of regions, to deliver more complex cognitive functions (as discussed above).

Shultz outlines a novel type of constructivist neural network that captures this idea. In knowledge-based cascade correlation (KBCC), the overall system tests and recruits networks from existing stock when they are required to support new computations. We speculate that a KBCC network architecture may capture, at least to some extent, emerging functionality in the prefrontal cortex (PFC). Converging lines of evidence show that the PFC has an important role in orchestrating other cortical regions during functional brain development (Johnson 2005; Thatcher 1992), as **Foster, van Eekelen, & Mattes** (**Foster et al.**) point out. We believe that constructivist neural networks of the kind described by Shultz are worth exploring as models of PFC functional development, in addition to the selective pruning process preferred by **Innocenti.** This leads us to a wider consideration of the nature of representations within the neuroconstructivist framework.

R4. Representation: Multiple modalities, flexibility, and abstraction

Our emphasis on the emergence of partial representations to drive behavior elicited several kinds of responses. **Bremner & Spence** argue for the importance of multisensory/multimodal experiences to deliver enriched representations that serve more than the child's immediate behavioral goals. **French** applauds the combination of dynamic systems theory and connectionist approaches inherent in the notion of partial representations. His research in analogy-making has led him to endorse the same idea (or "gospel") of flexible, context-dependent representations that are gradually constructed via a continual interaction between high- and low-level constraints. **Kotchoubey** argues that the very concept of representation implies a Cartesian theatre and the need for a homunculus to whom the content of representations is made available. Moreover, he wonders how "full" instead of partial representations might ever come about. For **Campos & Sotillo**, the emergence of specialized, context-dependent representations must be complemented by the later emergence of explicit representations that "permit independence from context, conscious reasoning, and interrepresentational relations," in line with the theory of representational redescription proposed by Karmiloff-Smith (1992). Indeed, the notion that context-dependent partial representations are the outcome of interactive specialization prompts further questions. For example, how does this square with the idea of the increasing *abstraction* of the child's representation over development? How does it fit with the idea of increasing *flexibility* in the child's use of knowledge, for example in the case of the development of meta-cognition? If anything, is this not an increase in *context independence*?

First, we agree with **Bremner & Spence** regarding the importance of multisensory and multimodal representations. We acknowledge that we may not have emphasized this sufficiently: Multimodal integration is a major constraint on development that played an important role in Piaget's theories and has been vindicated by neuroscientific research. We expect that in many cases, partial representations will be the consequence of detecting contingencies between multiple sets of sensory and motor information in regions where this information converges, and that richer information will aid in the detection of those contingencies. When a region receives multiple inputs, this is termed a *fan-in*. We also expect *fan-out* to be important – that is, where a region drives several outputs (see, e.g., the model of infant-object interactions described in chapt. 9 of Vol. I). Indeed, to the extent that the brain exhibits bidirectional connectivity, multiple outputs may be as influential as multiple inputs in driving the development of the representations in a given region.

Returning to our framework, we see multisensory integration as falling under the principle of embrainment,

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where the development and processing in one region is influenced by different brain regions (in this case, sensory cortices). This is similar to the sensorimotor model of the acquisition of speech sounds described in chapter 8 of Volume I. The same model has indeed been used to account for effects of multisensory integration (Westermann 2001). In this model two neural maps were linked via developing Hebbian connections. By exposing the model to multidimensional data sets with different correlational structures, Westermann demonstrated how perceptual change in each domain (such as categorical perception and perceptual prototypes) as well as multidimensional integration (the McGurk effect) can emerge from the gradual integration of unimodal data into a unified multimodal percept.

There is, however, a sense in which the idea of multisensory integration depends on the level of description. In general, we would expect the same neurocomputational mechanisms to operate between domains as within a single domain. Forming a (partial) representation requires learning about the statistics of patterns of presynaptic activity. The neuron doing the learning cannot know if the inputs it is receiving come from one or multiple domains. So the mechanism used must be the same in both cases. Multisensory integration is therefore a property that is salient at a particular (architectural) level of description.

Are the representations that result from the convergence of multiple senses any more abstract than those that result from a single sense? Possibly, in the sense that they are not bound to a single modality alone. A further sense in which increases in abstraction may be the consequence of development is the detection of higher-order invariances found in progressively higher layers of self-organizing neural networks, for example as observed in the mammalian visual system (see review in Ch. 6 of Vol. I). A more challenging prospect is to explain increases in flexibility in terms of context-dependent partial representations. We suspect the explanation will be in terms of the development of executive functioning, where flexibility is the ability to take advantage of existing knowledge in driving new behaviors. We are in agreement with **Foster et al.** on this point, as discussed in the previous section. Does the idea of flexibility necessarily imply context independence? We believe it does not. Equally, it may constitute the ability to switch back and forth between *different* contexts in a system whose representations remain context-bound.

Turning to the concerns of **Kotchoubey**, we do not agree that the concept of a representation or of an informational state necessarily requires the presence of an observer to read off the contents of the representation. The modified synapse is modified, whether anyone notices or not. Perhaps more important, it is not clear what empirical implications bear on this issue, one way or another. What consequences does it have for the developmental cognitive neuroscientist studying the mind whether representations require an observer or not? What consequences does it have for the developmental roboticist whose robot continues to show increasingly adaptive behavioral contingencies in interacting with its environment, even after its programmer has left the room?

In response to the idea of a partial representation, Kotchoubey justifiably poses the question of how an individual might ever attain a "full" representation of a concept. Here, we agree with **Innocenti** when he argues that "partial representations seem to be economical in terms of neural resources and are open to completion by developmental experience and/or learning, in adult life." We claim the following: For a representation to become full, the individual must integrate the partial representations across the entire range of contexts in which the concept is used. Different subsets of partial representations may be appropriate for different contexts and indeed, the only feature common to all contexts of the full representation may be the presence of a unifying label. In a sense, the generation of a full representation is similar to the process undertaken by a philosopher when he or she considers the coherence of a concept. What are all the applications of an idea? Philosophers, however, usually add a further proviso that concepts should *not* be context sensitive – a concept should mean same thing in all situations. While this proviso may optimize philosophical discourse, it may not be a principle to which the brain adheres.

Lastly, both **Bremner & Spence** and **Campos & Sotillo** raise the important issue of the outcome of development. The former argue that representational states are richer than those simply required to drive behavior in the moment, while the latter point to the importance of the late-developing property of explicitization that enables performance to break free from the context of its acquisition. In each case, development might be argued to have gone "beyond mastery" (Karmiloff-Smith 1992). We agree that there are key issues to be explored here. To these challenges, we might add behaviors that appear decoupled from the immediate environment, such as imagination and play. However, we would argue that all of these are amenable to the neuroconstructivist approach, with its appeal to multidisciplinary sources of evidence and formal specification of causal mechanism. We feel that the important ideas of Rivière, as discussed by Campos & Sotillo, may be in particular need of formal specification before they can be investigated at a neurocognitive level. For example, is *explicitization* a process intrinsic to a representation, where a system somehow self-organizes into a structure that generates new properties in the absence of a behavioral driver? Or is it more like an enabling of connectivity across systems, perhaps in particular to the language systems that drive (explicit) verbal report? When a child moves *beyond mastery*, is this more than a continued proactive tendency to query the environment for further potential sources of reward (novelty) – an idea well understood within the framework of reinforcement learning? Or does it refer to an internal computational process, for example a system-wide preference for global consistency across components of an interactive processing system, beyond the local consistency that enables a given subsystem to generate a behavior successfully?

R5. Genetics, lifespan, and evolution

French argues that we have given short shrift to the role of genetics in cognition, and views as "bordering on the incomprehensible" our statement that "in humans, genes provide only very broad sorts of constraints on the representations that emerge in cortex." We are sympathetic to his view; it

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is true that apart from a six-page section in chapter 1 of Volume I where we discuss the genetics of development, genes only appear intermittently throughout the volume. We have endeavored to rectify this in other publications (see Westermann et al. 2007, Fig. 4) where we emphasize the place of genes in our framework, and in particular the *probabilistic epigenesis* view of development (Gottlieb 1992; 2007). In the latter view, environmental and behavioral influences play a fundamental role in modulating the expression of genes. We expect that genes will exhibit a reliance on context (of other genes and of environments) for their causal effects similar to the contextual effects we observe at higher levels of description. We might term the contextual effect at the molecular level as *engenement*.

Despite our sympathies, there is also a sense in which we would defend our stance, and hold to our claim regarding the influence of genes on the emergence of representations in the cortex. While genes inevitably play an essential role in constructing and maintaining biological organisms from the moment of the fertilization of the egg onwards, the key issue at stake is the *specificity* of their influence on cognition. At present, while there are many suggestive correlations between gene variants or mutations and cognitive variability, there are few examples of explicit causal pathways that link these levels of description. We maintain that the optimum level of description to explain children's behavior is the cognitive level; the aim of neuroconstructivism is to seek constraints from other levels of description but not to reduce to them. And the causal chains linking genes and cognition are extremely indirect (as indeed they are between, for instance, sodium channels and cognition).

French mentions the FOXP2 gene, and this is an interesting example. A mutation of this gene produced an apparent specific deficit of speech and language with Mendelian inheritance in a British family. Computer simulations indicated that the human version of this gene may have appeared relatively recently on an evolutionary timescale, around the time language appeared in humans (see Marcus & Fisher 2003). However, subsequent research indicated that behavioral deficits were more widespread than language (affected family members also showed deficits in oral-facial movements, aspects of the perception of rhythm, production of rhythmic movements of the hand, and on average lower IQ than unaffected family members) and a range of structural brain differences were observed when affected family members were compared to unaffected members or controls (including in sensorimotor cortex, inferior temporal cortex, inferior frontal cortex, supplementary motor areas, the planum temporale, caudate nucleus, insula, putamen, and cerebellum) (see Vargha-Khadem et al. 2005). There is undeniably an uneven cognitive profile in affected family members, yet the effects of the single gene mutation were far from specific on either brain or behavior.

Indeed, Plomin and colleagues have argued both that relations between genes and cognition are likely to be many-to-many, so that each gene influences many cognitive processes and each cognitive process is influenced by many genes (e.g., Kovacs & Plomin 2006; Plomin & Kovacs 2005; see also Rutter 2007), and that gene expression is likely to be distributed widely throughout the brain rather than in specific regions. Two of the most studied genes within cognition, COMT and BDNF, have basic neural functions related to neurotransmitter metabolism and neural growth respectively, and their expression is found across cortex, cerebellum, caudate nucleus, amygdala, thalamus, and corpus callosum in both humans and mice (Kovas & Plomin 2006). Given the widespread expression of genes in the cortex, it might seem reasonable to conclude that they exert broad sorts of constraints on the representations that emerge. Of course, this picture may change. The field of genetic neuroimaging, which studies where and when various genes are expressed in the brain, is advancing rapidly. Nevertheless, while we have no doubt that it will soon be commonplace to include genotype information in studies of cognition (where it will pick up some proportion of the variance in behavior, along with other experimental factors), we believe it premature to identify the exact constraints that genes place on current theories of cognitive development.

Two commentaries urge us to expand the neuroconstructivist framework in other directions, to incorporate evolution (**Innocenti**) and to cover lifespan changes in cognition rather than just development (**Foster et al.**). Innocenti argues that an evolutionary perspective prompts a greater emphasis on selectionism, where evolution selects certain neural and/or cognitive structures and development makes a further selection from possible cognitive architectures depending on the (proactively defined) environment in which the organism finds itself. In discussing the apparent opposition between selectionism and constructivism, Innocenti draws a contrast between mechanisms of evolution where "the power of selection is unchallenged" and the developmental time frame within which proactivity (or active exploration) is more important. Recent advances in evolutionary theory as applied to behavior make us less confident about this contrast. The fact that the activity of animals, guided by their embodied brains, changes their environment is well known. For an extreme example, by damming a river, families of beavers change their local habitat, flora, and fauna for several generations. However, this process of niche construction generates a feedback process in evolution that has only recently been fully recognized (Olding-Smee et al. 2003). The implications of this new perspective are that all aspects of *niche construction*, including cultural processes in humans, can influence the selection of genetic variation. Thus, the view is that there is no longer just passive selection of genes by the environment, but rather that species can be considered to create the environment that subsequently selects particular genes in future generations. We speculate that different individuals, or groups of individuals, from a species may create novel niches in a manner similar to proactivity dependence. Thus, it is possible that a similar dynamic balance between selectionism and constructivism occurs in evolution as occurs in individual ontogeny.

For us, one of the key questions in considering the role of evolution on human cognition is to understand the levers available to evolution to selectively change aspects of the brain and/or cognitive system. Work by Finlay and colleagues (e.g., Finlay & Brodsky 2006; Finlay et al. 2001) demonstrates that a large amount of structural variance in mammalian brains can be explained by a small number of factors producing nonlinear scaling across species. This is consistent with the availability of only a

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small number of fairly general genetic levers to change brain structure rather than a panoply of individual levers that control specific brain areas or specific cognitive abilities. In particular, a many-to-many mapping between genes and cognition would make fashioning a particular cognitive process via evolution problematic. Let us say a given process increased fitness so that its genes were more likely to propagate in the population. Under a many-to-many mapping, the favored genes also contribute to the development and maintenance of a large number of other cognitive processes. Selection for the one would therefore entail selection for the many. In short, for both evolutionary and genetic contributions to developmental theory, the key issue is the specificity of the influences on higher cognition.

We are in agreement with **Foster et al.** that the neuroconstructivist framework may be profitably extended to consider changes over lifespan, where we believe the principles we have identified would be equally relevant (see the work discussed in Section 1). Craik and Bialystok (2006) recently discussed the generalized lack of an interface between development and aging research, and we agree that it is desirable to make links between developmental and lifespan changes in cognition. We would hesitate to take a modular view of the development of more fundamental cognitive abilities but agree with Foster et al. that chronotopy may be an important characteristic of the changes observed in adolescence related to prefrontal cortical functioning. The control, coordination, and flexible use of cognitive abilities is contingent on the development of those abilities (see also sect. 2). We also find appealing the idea that aging may appear to be the converse of interactive specialization, with poorer performance marked by increases in the number of areas activated in the brain. Such parallels must be treated with caution, however, since there may also be differences: Aging has differential effects across brain regions that find no correspondence in development (see, e.g., Burke & Barnes 2006), and aging may alter different neurocomputational properties than those responsible for changes in network specialization during development (Li et al. 2001).

R6. Chronotopy, disorders, subjectivity, complexity, and formal methods

For reasons of space, we deal with a remaining set of questions more briefly. Issues revolving around *chronotopy* arose in several contexts. **Bateson** highlights the role of competition in effective reductions in plasticity, where experiences of one kind can exclude subsequent experiences of another kind (see Richardson & Thomas 2008; Thomas & Johnson 2006; 2008, for further discussion of sensitive periods in development and their possible neurocomputational basis). As we saw above, **Foster et al.** discuss how the developmental changes in adolescence are reliant on the emergence of more fundamental cognitive abilities, and **Shultz** presents a possible computational formalism for exploiting previous knowledge in learning new abilities. Similarly, individual differences in aging indicate that the changes observed are to some extent dependent on the outcome of the developmental processes that preceded it (Stern 2002). For us, the key point here is that chronotopy should not be a descriptive principle – simply identifying the order of developmental events – but should allude to the causal mechanisms that explain the necessity of the ordering.

On the topic of *developmental disorders*, **Campos & Sotillo** rightly identify that the neuroconstructivist perspective has implications for intervention. In particular, it is important to focus as closely on "scores within the normal range" or apparently normally developing abilities as on the impairments, both to verify that these abilities are genuinely developing normally and to evaluate their potential to serve as scaffolding for apparently weaker abilities. For example, individuals with Williams syndrome are known to have visuospatial difficulties that can affect their navigation skills. This can have an impact on their everyday life – for example, on making independent trips to the shops. Language is held to be a relative strength in the disorder. But is language in Williams syndrome sufficiently well developed to accommodate a verbal strategy for navigating to the shops and back? (See Thomas 2004 for a discussion of the relation of neuroconstructivist research to intervention).

Here is it worth noting that Ramus (2004, p. 100) has characterized the neuroconstructivist approach as containing the following axiom: "no cognitive module in the adult mind can have originated in the newborn mind but must have been acquired through interaction with the environment," with the logical corollary that in the case of developmental disorders, "a cognitive module cannot be congenitally disrupted." We should stress that there is no such axiom. We are as keen as anyone to constrain our developmental accounts with as wide a range of empirical evidence from genetics, neurobiology, neuroimaging, computational modeling, and behavioral work as possible to build models that contain realistic constraints on the specificity of early deficits and their consequent effects on developmental trajectories. The neuroconstructivist perspective on developmental disorders is merely that a theory must specify starting conditions and the nature of the subsequent developmental process, and that both these aspects should be consistent with what is known from developmental cognitive neuroscience (Thomas & Karmiloff-Smith 2002).

Innocenti points out that developmental disorders stemming from atypical environments can be equally informative about development. While this was a class of disorder we identified in Chapter 11 of Volume I, we did not pursue it in the original volumes. Innocenti is right to highlight the importance of evidence from, for example, studies of deprivation and impoverished environments. Animal work also indicates how enriched environments can influence neural development, for example for rats reared in environments of varying complexity (reviewed in Praag et al. 2002; Rosenzweig 1996). Enriched environments have been observed to produce changes in cortical thickness, with larger cell bodies, more glial cells, and higher dendritic and synaptic density, as well as an increased rate of neurogenesis. The role of impoverished and enriched environments in modifying (or failing to modify) developmental trajectories is a key avenue of investigation.

Lickliter suggests that we underplayed the importance of *value* and *meaning* in the formation and maintenance of cognitive representations – in essence, the *subjectivity* of the individual. We agree with this criticism in that subjectivity, and the value system that defines it, was left implicit in the notion of proactivity. The work of Sporns on robotics in

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Volume II emphasizes how important the concept of value may be in determining the effective environment for the individual (e.g., Sporns 2007, p.184). Our review of behavioral genetics in the first chapter of Volume I noted that in twin studies, most of the variation in behavior attributable to the environment is unique to the individual (making identical twins look dissimilar) rather than shared (causing both identical and fraternal twins to look similar). Therefore, even when the environment appears similar (such as growing up in the same family or going to the same school), individuals experience it differently.

A number of the commentaries remark on our preference for the use of *formal modeling* to specify causal mechanisms underlying developmental change. In some cases, the comments are optimistic on the gains that formal modeling will provide (e.g., **Bateson**), in other cases, they are pessimistic (e.g., **Lickliter**). For Lickliter, the difficulty lies in closed or bidirectional causal loops between organism and environment at multiple levels, producing "mind-boggling combinatorial complexity" and "dizzyingly complex multidetermined phenomena." In some ways, we agree with this view. The complexity of the ongoing interactions at multiple levels of description makes analysis extremely problematic. **Pribram** also highlights the implication of *complexity* in the context of nonlinear dynamics. Formal methods can at least offer a chance to understand the emergent properties of such interactions, for example as illustrated by Sirois and Mareschal's model of infant habituation (2004). At the very least, formal models force the investigator to understand the complexity of the theory that is being proposed. A term like *proactivity* is easy to postulate at the qualitative level, but formal modeling uncovers serious issues associated with it. Allowing a learning system to determine the nature of its training set by its actions on an environment places it at great risk of instability. As **Ferber** recognizes, this has much in common with the problems faced by engineering control systems that operate via feedback (see, e.g., Mees 1981). Without damping, a proactive system may oscillate between improving on different, inconsistent parts of the training set. Without time-sensitive changes of internal state, the system may lapse into locally stable solutions that are far from optimal for the problem it faces. The fact that formal approaches reveal such implications confirms that, however high the Everest of development may be, formal modeling leads us uphill.

R7. Omissions

As we stated in the preface to Volume I, too many great people have influenced our thinking for us to be able to acknowledge each directly. But we are grateful for the chance to acknowledge some of them here, in response to the influences recognized by the commentators. For example, **French** points out that we had not cited Hebb (1949) – so pervasive was his influence on our thinking that we failed to cite him! French also notes the similarities of our machine-learning analysis of development (see Mareschal & Thomas 2007) to that proposed by Regier (1996), which we are happy to acknowledge. Similarly, **Lickliter** points out the importance of the work of Walter Freeman (2001) on the relation between representation and meaning. While **Bateson** agrees with much of what we say, he chastises us for not properly acknowledging the contributions of many developmentally inclined ethologists and neuroethologists. Of course, it is a hazard in an interdisciplinary book such as this that experts from any single one of the constituent fields may feel that their discipline has not been adequately represented in the mix. However, this particular criticism stings hard because we consider ethology (as the behavioral development of animals in their natural environment) a critical and vital foundation stone for our book. For example, at the start of chapter 4 of Volume I on embodiment we clearly root this idea in classical ethology, giving examples from the work of Tinbergen, Ewert, and Beer among others. We fully acknowledge that there could have been many other names added to this list, but our primary objective was to then merge these ideas with those from robotics and artificial intelligence, and not to provide a scholarly review of the ethology literature. For reasons of readability, therefore, we gave only a few examples. However, we welcome the opportunity to clarify the seminal importance, and influence on our thinking, of ethologists such as Bateson, Oyama, Hinde, and Gottlieb (the latter two already being cited in the book). For at least one of the authors (M.H.J.), this is the single most important intellectual tradition that influences our work. That it continues to be so is evident from our discussion of niche construction in Section R4.

R8. Conclusion

We are glad to learn from the contributors how they believe the neuroconstructivist framework can be expanded. The *Neuroconstructivism* books are the first steps on a long road. We have aimed to provide a framework within which to think about development and the factors affecting it. We believe that this framework is a powerful one that integrates disparate fields and levels of description into a unified whole. Many researchers can contribute to this framework from their own areas of specialization. The commentators offer clear pointers of the directions in which neuroconstructivism can expand: a more detailed consideration of the theory of interactive specialization; specification of the relation between the emergence of partial representations and developmental changes in abstraction and cognitive flexibility, including the role of the prefrontal cortex; the important role of genetics in explanations of development; the function of value and subjective experience in proactivity; changes in cognition across lifespan, including the putative reorganization in adolescence and the processes underlying cognitive decline in the aging population; the effects of atypical environments in deflecting developmental trajectories; the implications of a neuroconstructivist analysis of developmental disorders for intervention; and, at the formal level, the implications of closed causal loops between the individual and his/her environment. With such avenues to explore, we believe that the multidisciplinary study of development has a rich future in the twenty-first century.

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NOTE

1. Imagine a layer of processing units fed by two banks of input units (A and B) and driving a single bank of output units C. The layer of processing units (the 'region') performs categorisations over the activity arriving from input A, differentially driving the bank of output units C, depending on the particular pattern arriving from A. It is straightforward to demonstrate that the categorisations that the region carries out on A can be modulated – indeed completely changed – by activation arriving from input bank B. The modulation of the region's computational properties can occur without any changes to the network's connection weights, merely via changes in its non-linear activation dynamics (see, for example, Rogers & McClelland 2004).

References

Letters "a" and "r" appearing before authors' initials refer to target article and response, respectively.

Adolphs, R. (2003) Cognitive Neuroscience of Human Social Behavior. *Nature Reviews Neuroscience* 4:165–78. [aSS]

Alba, Richard D. (1973) A graph-theoretic definition of a sociometric clique. *Journal of Mathematical Sociology* 3:113–26. [MLA]

Als, H., Duffy, F. H., McAnulty, G. B., Rivkin, M. J., Vajapeyam, S., Mulkern, R. V., Warfield, S. K., Huppi, P. S., Butler, S. C., Conneman, N., Fischer, C. & Eichenwald, E. C. (2004) Early experience alters brain function and structure. *Pediatrics.* 113(4):846–57. [SGF]

Anderson, M. L. (2007a) Evolution of cognitive function via redeployment of brain areas. *The Neuroscientist* 13(1):13–21. [MLA]

(2007b) Massive redeployment, exaptation, and the functional integration of cognitive operations. *Synthese* 159(3):329–45. [MLA]

(2007c) The massive redeployment hypothesis and the functional topography of the brain. *Philosophical Psychology* 21(2):143–74. [MLA]

Anderson, M. L., Brumbaugh, J. & Suben, A. (in press) Investigating functional cooperation in the human cortex with simple graph-theoretic methods. In: *Computational neuroscience*, ed. W. A. Chaovalitwongse, P. Pardalos & P. Xanthopoulos. Springer Verlag. [MLA]

Anokhin, P. K. (1974) *Biology and neurophysiology of the conditioned reflex and its role in adaptive behavior*, trans. R. Dartau, J. Epp & V. Kirilcuk. Pergamon Press. [BK]

Armstrong, R. C. & Montminy, M. R. (1993) Transsynaptic control of gene expression. *Annual Review Neuroscience* 16:17–29. [aSS]

Bahrick, L. E., Lickliter, R. & Flom, R. (2004) Intersensory redundancy guides infants' selective attention, perception, and cognition in infancy. *Current Directions in Psychological Science* 13:99–102. [AJB]

Baillargeon, R. (1987) Object permanence in 3 1/2- and 4 1/2-month-old infants. *Developmental Psychology* 23:655–64. [TRS]

Ballard, D. H., Hayhoe, M. M., Pook, P. K. & Rao, R. P. N. (1997) Deictic codes for the embodiment of cognition. *Behavioral and Brain Sciences* 20:723–67. [aSS]

Baluja, S. & Fahlman, S. E. (1994) Reducing network depth in the cascade-correlation learning architecture. (Technical Report CMU-CS-94-209). School of Computer Science, Carnegie Mellon University. [TRS]

Bandura, A. (1986) *The social foundations of thought and action*. Prentice-Hall. [aSS]

Baron-Cohen, S. (1999) Does the study of autism justify minimalist innate modularity? *Learning and Individual Differences* 10:179–91. [aSS]

Baron-Cohen, S., Tager-Flusberg, H. & Cohen, H. J., eds. (1993) *Understanding other minds: Perspectives from autism.* Oxford University Press. [aSS]

Bateson, P., ed. (1991) *The development and integration of behaviour*. Cambridge University Press. [PB]

Bateson, P., Barker, D., Clutton-Brock, T., Deb, D., D'Udine, B., Foley, R. A., Gluckman, P., Godfrey, K., Kirkwood, T., Lahr, M. M., McNamara, J., Metcalfe, N. B., Monaghan, P., Spencer, H. G. & Sultan, S. E. (2004) Developmental plasticity and human health. *Nature* 430:419–21. [PB]

Bateson, P. & Horn, G. (1994) Imprinting and recognition memory: A neural net model. *Animal Behaviour* 48:695–715. [PB]

Becker, L. E., Armstrong, D. L. & Chan, F. (1986) Dendritic atrophy in children with Down's syndrome. *Annals of Neurology* 20:520–26. [aSS]

Berbel, P., Obrego, M. J., Bernal, J., Escobar del Rey, F. & Morreale de Escobar, G. (2007) Iodine supplementation during pregnancy: A public health challenge. *Trends in Endocrinology and Metabolism* 18:338–43. [GMI]

Berk, L. & Gavin, R. (1984) Development of private speech among low-income Appalachian children. *Developmental Psychology* 20:271–86. [aSS]

Bickhard, M. H. (2005) Consciousness and reflective consciousness. *Philosophical Psychology* 18(2):205–18. [BK]

Bogartz, R. S., Shinskey, J. L. & Speaker, C. J. (1997) Interpreting infant looking: The event set x event set design. *Developmental Psychology* 33:408–22. [aSS]

Boysson-Bardies, B., Halle, P., Sagart, L. & Durand, C. (1989) A cross-linguistic investigation of vowel formants in babbling. *Journal of Child Language* 16:1–17. [aSS]

Bremner, A. J., Mareschal, D., Lloyd-Fox, S. & Spence, C. (2008) Spatial localization of touch in the first year of life: Early influence of a visual spatial code and the development of remapping across changes in limb position. *Journal of Experimental Psychology: General* 137:149–62. [AJB]

Brooks, R. A. (1990) Elephants don't play chess. *Robotics and Autonomous Systems* 6:3–15. [RMF]

Burke, S. N. & Barnes, C. A. (2006) Neural plasticity in the ageing brain. *Nature Neuroscience* 7(1):30–40. [rMSCT]

Campos, J. J., Anderson, D. I., Barbu-Roth, M. A., Hubbard, E. M., Hertenstein, M. J. & Witherington, D. (2000) Travel broadens the mind. *Infancy* 1:149–219. [aSS]

Campos, R. (in preparation) Construyendo mentes: El desarrollo de la comprensión de estados mentales en niños con síndrome de Williams y niños sin alteraciones. (Unpublished thesis manuscript, Universidad Autónoma de Madrid). [RC]

Casey, B. J., Giedd, J. N. & Thomas, K. M. (2000) Structural and functional brain development and its relation to cognitive development. *Biological Psychology* 54:241–57. [JF]

Cashon, C. H. & Cohen, L. B. (2000) Eight-month-old infants' perceptions of possible and impossible events. *Infancy* 1:429–46. [aSS]

Castles, A. & Coltheart, M. (1993) Varieties of developmental dyslexia. *Cognition* 47:149–80. [aSS]

Chiel, H. J. & Beer, R. D. (1997) The brain has a body: Adaptive behavior emerges from interactions of nervous system, body, and environment. *Trends in Neurosciences* 20:553–57. [RL]

Chugani, D. C., Muzik, O., Behen, M., Rothermel, R., Janissee, J. J., Lee, J. & Chugani, H. T. (1999) Developmental changes in serotonin synthesis capacity in autistic and non-autistic children. *Annals of Neurology* 45:287–95. [aSS]

Clark, A. (1997) *Being There*. MIT Press. [aSS]

Clark, A. & Thornton, C. (1997) Trading spaces: Computation, representation and the limits of uninformed learning. *Behavioral and Brain Sciences* 20:57–66. [aSS]

Clifton, R. K. & Nelson, M. N. (1976) Developmental study of habituation in infants: The importance of paradigm, response system, and state. In: *Habituation: Perspectives from child development, animal behavior and neurophysiology*, ed. T. J. Tighe & R. N. Leaton, pp. 159–205. Erlbaum. [aSS]

Cohen, L. B. (1972) Attention-getting and attention-holding process of infant visual preferences. *Child Development* 43:869–79. [aSS]

Cohen, L. B. & Cashon, C. H. (2003) Infant perception and cognition. In: *Handbook of psychology: Developmental psychology*, vol. 6, ed. R. Lerner, A. Easterbrooks, & J. Mistry, pp. 65–89. Wiley. [aSS]

Cohen, L. B. & Marks, K. S. (2002) How infants process addition and subtraction events. *Developmental Science* 5:186–201. [aSS]

Craik, F. I. M. & Bialystok, E. (2006) Cognition through the lifespan: Mechanisms of change. *Trends in Cognitive Sciences* 10(3):131–38. [rMSCT]

Crowley, J. C. & Katz, L. C. (1999) Development of ocular dominance columns in the absence of retinal input. *Nature Neuroscience* 2:1125–30. [aSS]

Csibra, G. & Gergely, G. (2006) Social learning and social cogniton: The case for pedagogy. In: *Processes of Change in Brain and Cognitive Development. Attention and Performance XXI*, ed. M. H. Johnson & Y. Munakata. Oxford University Press. [aSS]

De Haan, M. (2007) *Infant EEG and event-related potentials.* Psychology Press. [rMSCT]

Dehaene, S (2003). Natural born readers. *New Scientist*, 5th July 2003, no. 2402, 30–33. [aSS]

Dehaene, S., Le Clec'H., Poline, J-P., Le Bihan, D. & Cohen, L. (2002) The visual word form area: A prelexical representation of visual words in the fusiform gyrus. *NeuroReport* 13:321–25. [aSS]

Deruelle, C., Mancini, J., Livet, M. O., Casse-Perrot, C. & de Schonen, S. (1999) Configural and local processing of faces in children with Williams syndrome. *Brain and Cognition* 41:276–98. [aSS]

Desimone, R. (1996) Neural mechanisms for visual memory and their role in attention. *Proceedings of the National Academy of Sciences USA* 93:13494–99. [aSS]

Desimone, R. & Duncan, J. (1995) Neural mechanisms of selective visual attention. *Annual Review of Neuroscience* 18:193–222. [aSS]

https://doi.org/10.1017/S0140525X08004184 Published online by Cambridge University Press

Diamond, A. (1991) Frontal lobe involvement in cognitive changes during the first year of life. In: *Brain maturation and cognitive development: A comparative and cross-cultural perspective*, ed. K. R. Gibson & A. C. Petersen, pp. 127–80. Aldine de Gruyter. [aSS]

Dickerson, B. C., Salat, D. H., Greve, D. N., Chua, E. F., Rand-Giovannetti, E., Rentz, D. M., Bertram, L., Mullin, K., Tanzi, R. E., Blacker, D., Albert, M. S. & Sperling, R. A. (2005) Increased hippocampal activation in mild cognitive impairment compared to normal aging and AD. *Neurology* 65:404–11. [JF]

Driver, J., Davis, G., Russell, C., Turatto, M. & Freeman, E. (2001) Segmentation, attention and phenomenal visual objects. *Cognition* 80:61–95. [aSS]

Duffy, F. H., Als, H. & McAnulty, G. B. (2003) Infant EEG spectral coherence data during quiet sleep: Unrestricted principal components analysis – relation of factors to gestational age, medical risk, and neurobehavioral status. *Clinical Electroencephalography* 34(2):54–69. [SGF]

Durston, S., Davidson, M. C., Tottenham, N., Galvan, A., Spicer, J., Fossella, J. A. & Casey, B. J. (2006) A shift from diffuse to focal cortical activity with development. *Developmental Science* 9(1):1–8. [rMSCT]

Egri, L. & Shultz, T. R. (2006) A compositional neural-network solution to prime-number testing. In: *Proceedings of the Twenty-eighth Annual Conference of the Cognitive Science Society*, ed. R. Sun & N. Miyake, pp. 1263–68. Erlbaum. [TRS]

Eimas, P. D., Siqueland, E. R., Jusczyk, P. & Vigorito, J. (1971) Speech perception in infants. *Science* 171:303–306. [aSS]

Elman, J., Bates, E., Johnson, M. H., Karmiloff-Smith, A., Parisi, D. & Plunkett, K. (1996) *Rethinking innateness: A connectionist perspective on development*. MIT Press. [aSS]

Fahlman, S. E. & Lebiere, C. (1990) The cascade-correlation learning architecture. In: *Advances in neural information processing systems 2*, ed. D. S. Touretzky, pp. 524–32. Morgan Kaufmann. [TRS]

Fantz, R. L. (1964) Visual experience in infants: Decreased attention to familiar patterns relative to novel ones. *Science* 146:668–70. [aSS]

Farroni, T., Csibra, G., Simion, F. & Johnson, M. H. (2002) Eye contact detection in humans from birth. *Proceedings of the National Academy of Sciences* 99:9602–605. [aSS]

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

Ferber, S. G. & Makhoul, I. R. (2004) The effect of skin-to-skin contact (kangaroo care) shortly after birth on the neurobehavioral responses of the term newborn: A randomized, controlled trial. *Pediatrics* 113(4):858–65. [SGF]

(2008) Neurobehavioural assessment of skin-to-skin effects on reaction to pain in preterm infants: A randomized, controlled within-subject trial. *Acta Paediatrica* 97(2):171–76. [SGF]

Finlay, B. L. & Brodsky, P. B. (2006) Cortical evolution as the expression of a program for disproportionate growth and the proliferation of areas. In: *Evolution of nervous systems*, ed. J. H. Kaas, pp. 73–96. Oxford University Press. [rMSCT]

Finlay, B. L., Darlington, R. D. & Nicastro, N. (2001) Developmental structure of brain evolution. *Behavioral and Brain Sciences* 24:263–308. [rMSCT]

Fodor, J. A. (1975) *The language of thought*. Harvard University Press. [aSS]

Fodor, J. A. & Pylyshyn, Z. (1988) Connectionism and cognitive architecture: A critique. *Cognition* 28:3–71. [aSS]

Foldiak, P. (1991) Learning invariance from transformation sequences. *Neural Computation* 3:194–200. [aSS]

Foster, J. K. (1997) The "locality assumption": Lessons from history and neuroscience? *Behavioral and Brain Sciences* 20:518. [JF]

Freeman, W. (2001) *How brains make up their minds*. Columbia University Press. [RL, rMSCT]

Ghosh, A., Carnahan, J. & Greenberg, M. E. (1994) Requirement for BDNF in activity-dependent survival of cortical neurons. *Science* 263:1618–23. [aSS]

Gibson, E. J. (1969) *Principles of perceptual learning and development*. Appleton-Century-Crofts. [AJB]

(1979) *The ecological approach to visual perception*. Houghton Mifflin. [aSS]

(1982) The concept of affordances in development: The renascence of functionalism. In: *The concept of development. The Minnesota Symposia On Child Psychology*, ed. W. A. Collins, pp. 55–82. Erlbaum. [aSS]

Goldfield, E. C., Kay, B. & Warren, W. (1993) Infant bouncing: The assembly and tuning of an action system. *Child Development* 64:1128–42. [aSS]

Goldstein, D. G. & Gigerenzer, G. (2002) Models of ecological rationality: The recognition heuristic. *Psychological Review* 109:75–90. [aSS]

Goodman, C. S. & Shatz, C. J. (1993) Developmental mechanisms that generate precise patterns of neuronal connectivity. *Cell* 72:77–98. [aSS]

Goswami, U. (2002) Phonology, reading development and dyslexia: A cross-linguistic perspective. *Annals of Dyslexia* 52:1–23. [aSS]

(2003) Phonology, learning to read and dyslexia: A cross-linguistic analysis. In: *Dyslexia: Different brain, different behavior*, ed. V. Csepe, pp. 1–40. Kluwer Academic. [aSS]

Gottlieb, G. (1992) *Individual development and evolution*. Oxford University Press. [rMSCT]

(1997) *Synthesizing nature/nurture*. Erlbaum. [RL]

(2007) Probabilistic epigenisis. *Developmental Science* 10:1–11. [aSS, rMSCT]

Gottlieb, G. & Halpern, C. T. (2002) A relational view of causality in normal and abnormal development. *Developmental Psychopathology* 14:421–35. [RL]

Greenwood, P. M. (2007) Functional plasticity in cognitive aging: Review and hypothesis. *Neuropsychology* 21:657–73. [JF]

Grice, S., Spratling, M. W., Karmiloff-Smith, A., Halit, H., Csibra, G., de Haan, M. & Johnson, M. H. (2001) Disorders visual processing and oscillatory brain activity in autism and Williams syndrome. *NeuroReport* 12:2697–700. [aSS]

Hamalainen, A., Pihlajamaki, M., Tanila, H., Hanninen, T., Niskanen, E., Tervo, S., Karjalainen, P. A., Vanninen, R. L. & Soininen, H. (2007) Increased fMRI responses during encoding in mild cognitive impairment. *Neurobiology of Aging* 28:1889–903. [JF]

Harm, M. W. & Seidenberg, M. S. (2004) Computing the meaning of words in reading: Cooperative division of labor between visual and phonological processes. *Psychological Review* 111:662–720. [aSS]

Hebb, D. O. (1949) *The organization of behavior*. Wiley. [RMF, rMSCT]

Heit, E. (1994) Models of the effects of prior knowledge on category learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 20:1264–82. [TRS]

Herrmann, K. & Shatz, C. J. (1995) Blockade of action potential activity alters initial arborization of thalamic axons within layer 4. *Proceedings of the National Academy of Sciences* 92:11244–48. [aSS]

Hofer, M. A. (1994) Early relationships as regulators of infant physiology and behavior. *Acta Paediatric Supplement* 397:9–18. [SGF]

Howlin, P., Baron-Cohen, S. & Hadwin, J. (1999) *Teaching children with autism to mind-read*. Wiley. [RC]

Hubel, D. H. & Wiesel, T. N. (1963) Shape and arrangement of columns in cat's striate cortex. *Journal of Physiology* 165:559–68. [aSS]

Humphreys, G. W. & Riddoch, M. (2003) From what to where. *Psychological Science* 14:487–92. [aSS]

Hutchins, E. (1995) *Cognition in the wild*. MIT Press. [aSS]

Huttenlocher, P. R. & Dabholkar, A. S. (1997) Regional differences in synaptogenesis in human cerebral cortex. *Journal of Comparative Neurology* 387:167–78. [JF]

Innocenti, G. M. (2006) The role of transient, exuberant axonal structures in the evolution of Cerebral Cortex. In: *The evolution of the nervous system*, ed. John Kaas, pp. 259–67. Academic Press. [GMI]

(2007) Subcortical regulation of cortical development. Some effects of early cortical deprivation, ed. C. Von Hofsten & K. Rosander. *Progress in Brain Research* 164:23–37. [GMI]

Innocenti, G. M. & Price D. J. (2005) Exuberance in the development of cortico-cortical networks. *Nature Reviews Neuroscience* 6:955–64. [GMI]

Jakobson, R. (1941) *Child language, aphasia and phonological universals*. Mouton. (English translation by A. R. Keiler, 1968.) [aSS]

Järvilehto, T. (2001) Consciousness "within" or "without"? Review of *Modeling Consciousness Across The Disciplines. Journal of Consciousness Studies* 8(4):89–93. [BK]

Johnson, M. H. (2000) Functional brain development in infants: Elements of an interactive specialization framework. *Child Development* 71:75–81. [rMSCT]

(2001) Functional brain development in humans. *Nature Reviews Neuroscience* 2:475–83. [rMSCT]

(2004) Plasticity and functional brain development: The case of face processing. In: *Attention & Performance XX: Functional neuroimaging of visual cognition*, ed. N. Kanwisher & J. Duncan, pp. 257–63: Oxford University Press. [aSS]

(2005) *Developmental cognitive neuroscience*, 2nd edition. Blackwell. [aSS, rMSCT]

Johnson, M. H., Dziurawiec, S., Ellis, H. D. & Morton, J. (1991) Newborns preferential tracking of face-like stimuli and its subsequent decline. *Cognition* 40:1–19. [aSS]

Johnson, M. H. & Morton, J. (1991) *Biology and Cognitive Development: The Case of Face Recognition*. Blackwell. [aSS]

Johnson, M. H. & Munakata, Y. (2005) Processes of change in brain and cognitive development. *Trends in Cognitive Sciences* 9:152–58. [aSS]

Johnson, M. H. & Vecera, S. P. (1996) Cortical differentiation and neurocognitive development: The parcellation conjecture. *Behavioural Processes* 36:195–212. [aSS]

Johnston, T. D. & Edwards, L. (2002) Genes, interactions, and development. *Psychological Review* 109:26–34. [RL]

Jordan, J. S. (2000) The world in the organism: Living systems are knowledge. *Psycholoque* 11:113. [BK]

Kaldy, Z. & Sigala, N. (2004) The neural mechanisms of object working memory: What is where in the infant brain? *Neuroscience and Biobehavioural Reviews* 28:113–21. [aSS]

https://doi.org/10.1017/S0140525X08004184 Published online by Cambridge University Press

Karmiloff-Smith, A. (1992) *Beyond modularity: A developmental perspective on cognitive science*. MIT Press. [RC, aSS, rMSCT]
(1998a) Development itself is the key to understanding developmental disorders. *Trends in Cognitive Sciences* 2:389–98. [aSS]
(1998b) Is atypical development necessarily a window on the normal mind/brain?: The case of Williams syndrome. *Developmental Science* 1(2):273–77. [RC]
(2006) Modules, genes, and evolution: What have we learned from atypical development? In: *Attention & Performance XXI: Processes of change in brain and cognitive development*, ed. Y. Munakata, & M. H. Johnson, pp. 563–83. Oxford University Press. [RC]
Karmiloff-Smith, A., Grant, J., Berthoud, I., Davies, M., Howlin, P. & Udwin, O. (1997) Language and Williams syndrome: How intact is "intact"? *Child Development* 68(2):246–62. [RC]
Karmiloff-Smith, A., Thomas, M. S. C., Annaz, D., Humphreys, K., Ewing, S., Grice, S., Brace, N., Van Duuren, M., Pike, G. & Campbell, R. (2004) Exploring the Williams syndrome face processing debate: The importance of building developmental trajectories. *Journal of Child Psychology and Psychiatry and Allied Disciplines* 45:1258–74. [aSS]
Karni, A., Meyer, G., Jezzard, P., Adams, M. M., Turner, R. & Ungerleider, L. G. (1995) Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature* 377:155–58. [aSS]
Kaufmann, W. E. & Moser, H. W. (2000) Dendritic anomalies in disorders associated with mental retardation. *Cerebral Cortex* 10:981–91. [aSS]
Keller, E. F. (2002) *Making sense of life: Explaining biological development with models, metaphors, and machines*. Harvard University Press. [RL]
Kingsbury, M. A., Lettman, N. A. & Finlay, B. L. (2002) Reduction of early thalamic input alters adult corticocortical connectivity. *Brain Research Developmental Brain Research* 138:35–43. [GMI]
Koopmans-van Beinum, F. J., Clement, C. J. & van den Dikkenberg-Pot, I. (2001) Babbling and the lack of auditory speech perception: A matter of coordination? *Developmental Science* 4:61–70. [aSS]
Kovacs, Y. & Plomin, R. (2006) Generalist genes: Implications for the cognitive sciences. *Trends in Cognitive Sciences* 10(5):198–203. [rMSCT]
Kuhl, P. K. & Melzoff, A. N. (1996) Infant vocalization in response to speech: Vocal imitation and developmental change. *Journal of the Acoustic Society* 100:2425–38. [GMI]
Lamme, V. A. F. & Roelfsema, P. R. (2000) The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences* 23:571–79. [aSS]
Lenneberg, E. (1967) *Biological foundations of language*. Wiley. [aSS]
Leslie, A., Xu, F., Tremoulet, P. & Scholl, B. (1998) Indexing and the object concept: "What" and "where" systems in infancy. *Trends in Cognitive Sciences* 2:10–18. [aSS]
Lewkowicz, D. J. (2000) Perceptual development: Visual, auditory and speech perception in infancy. *American Journal of Psychology* 113:488–500. [AJB]
Li, S-C., Lindenberger, U. & Sikstrom, S. (2001) Aging cognition: From neuromodulation to representation. *Trends in Cognitive Sciences* 5(11):479–86. [rMSCT]
Lickliter, R. & Honeycutt, H. (2003) Developmental dynamics: Toward a biologically plausible evolutionary psychology. *Psychological Bulletin* 129:819–35. [RL]
Liu, H.-M., Kuhl, P. & Tsao, F.-M. (2003) An association between mothers' speech clarity and infants' speech discrimination skills. *Developmental Science* 6:F1–F10. [aSS]
Luna, B., Garver, K. E., Urban, T. A., Lazar, N. A. & Sweeney, J. A. (2004) Maturation of cognitive processes from late childhood to adulthood. *Child Development* 75:1357–72. [JF]
Luna, B. & Sweeney, J. A. (2004) The emergence of collaborative brain function – fMRI studies of the development of response inhibition. *Annals of the New York Academy of Sciences* 1021:296–309. [JF]
Manis, F. R., Seidenberg, M. S., Doi, L. M., McBride-Chang, C. & Petersen, A. (1996) On the bases of two subtypes of developmental dyslexia. *Cognition* 58:157–95. [aSS]
Marcus, G. F. & Fisher, S. E. (2003) FOXP2 in focus: What can genes tell us about speech and language? *Trends in Cognitive Sciences* 7(6):257–62. [rMSCT]
Mareschal, D. & Bremner A. J. (2005) When do 4-month-olds remember the "what" and "where" of hidden objects? In: *Attention & performance XXI: Processes of change in brain and cognitive development*, ed. M. H. Johnson & Y. Munakata, pp. 427–47. Oxford University Press. [aSS]
Mareschal, D. & Johnson, M. H. (2003) The "what" and "where" of infant object representations. *Cognition* 88:259–76. [aSS]
Mareschal, D., Johnson, M. H., Sirois, S., Spratling, M., Thomas, M. & Westermann, G. (2007a) *Neuroconstructivism, vol. I: How the brain constructs cognition*. Oxford University Press. [MLA, AJB, PB, RC, JF, RMF, SGF, GMI, BK, RL, KP, aSS, TRS]
Mareschal, D., Sirois, S. Westermann, G. & Johnson, M. H. (2007b) *Neuroconstructivism, vol. II: Perspectives and prospects*. Oxford University Press. [JF, RMF, SGF, KP, aSS]
Mareschal, D., Plunkett, K. & Harris, P. (1999) A computational and neuropsychological account of object-oriented behaviours in infancy. *Developmental Science* 2:306–17. [aSS, TRS]
Mareschal, D. & Shultz, T. R. (1996) Generative connectionist architectures and constructivist cognitive development. *Cognitive Development* 11:571–605. [aSS]
Mareschal, D. & Thomas, M. S. C. (2007) Computational modeling in developmental psychology. *IEEE Transactions on Evolutionary Computation (Special Issue on Autonomous Mental Development)* 11(2):137–50. [rMSCT]
Maris, M. & te Boekhorst, R. (1996) Exploiting physical constraints: heap formation through behavioural error in a group of robots. In: *Proceedings of the IROS '96, IEEE/RSJ International Conference on Intelligent Robots and Systems*. November 4–8, Osaka, Japan. [aSS]
Marr, D. (1982) *Vision*. W. Freeman. [RMF, aSS]
Maturana, H. R. & Varela, F. J. (1980) *Autopoiesis and cognition: The realization of the living*. Reidel. [BK]
McCall, R. B., Kennedy, C. B. & Applebaum, M. I. (1977) Magnitude of discrepancy and the distribution of attention in infants. *Child Development* 48:772–86. [aSS]
McCandliss, B. D., Cohen, L. & Dehaene, S. (2003) The visual word form area: Expertise for reading in the fusiform gyrus. *Trends in Cognitive Sciences* 7:293–99. [aSS]
McClelland, J. L., Fieza, J. A. & McCandliss, B. D. (2002) Teaching the /r/-/l/ discrimination to Japanese adults: Behavioral and neural aspects. *Physiology & Behavior* 77:657–62. [aSS]
Mees, A. I. (1981) *Dynamics of feedback systems*. Wiley. [rMSCT]
Merigan, W. H. & Maunsell, J. H. R. (1993) How parallel are the primate visual pathways. *Annual Review of Neuroscience* 16:369–402. [aSS]
Morton, J. & Johnson, M. H. (1991) CONSPEC and CONLERN: A two-process theory of infant face recognition. *Psychological Review* 98:164–81. [aSS]
Navon, D. (1981) The forest revisited: More on global precedence. *Psychological Bulletin* 43:1–32. [BK]
Neil, P. A., Chee-Ruiter, C., Scheier, C., Lewkowicz, D. J. & Shimojo, S. (2006) Development of multisensory spatial integration and perception in humans. *Developmental Science* 9:454–64. [AJB]
Nelson, C. A. (1995) The ontogeny of human memory: A cognitive neuroscience perspective. *Developmental Psychology* 31:723–38. [aSS]
Nelson, C. A. & Monk, C. S. (2001) The use of event-related potentials in the study of cognitive development. In: *Handbook of developmental cognitive neuroscience*, ed. C. A. Nelson & M. Luciana, pp. 125–36. MIT Press. [rMSCT]
Nelson, K. (2007) *Young minds in social worlds*. Harvard University Press. [RL]
Neville, H. J. & Lawson, D. (1987) Attention to central and peripheral visual space in a movement detection task: An event-related potential and behavioral study. II. Congenitally deaf adults. *Brain Research* 405:268–83. [aSS]
Olding-Smee, J., Laland, K. & Feldman, M. (2003) *Niche construction: The neglected process in evolution*. Princeton University Press. [rMSCT]
O'Leary, D. D. M. & Stanfield, B. B. (1989) Selective elimination of axons extended by developing cortical neurons is dependent on regional locale: Experiments utilizing fetal cortical transplants. *Journal of Neuroscience* 9:2230–46. [aSS]
Oliver, A., Johnson, M. H., Karmiloff-Smith, A. & Pennington, B. (2000) Deviations in the emergence of representations: A neuroconstructivist framework for analysing developmental disorders. *Developmental Science* 3:1–23. [aSS]
Oller, D. K. & Eilers, R. E. (1988) The role of audition in infant babbling. *Child Development* 59:441–49. [aSS]
Oppenheim, R. W. (1991) Cell death during development of the nervous system. *Annual Review Neuroscience* 14:453–501. [aSS]
Paterson, S. J., Brown, J. H., Gsödl, M. K., Johnson, M. H. & Karmiloff-Smith, A. (1999) Cognitive modularity and genetic disorders. *Science* 286:2355–58. [aSS]
Paus, T. (2005) Mapping brain maturation and cognitive development during adolescence. *Trends in Cognitive Sciences* 9:60–68. [JF]
Pazzani, M. J. (1991) Influence of prior knowledge on concept acquisition: Experimental and computational results. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 17:416–32. [TRS]
Pennington, B. F. (1999) Dyslexia as a neurodevelopmental disorder. In: *Neurodevelopmental disorders*, ed. H. Tager-Flusberg, pp. 307–30. MIT Press. [aSS]
Petersen, S. E., Van Mier, H., Fiez, J. A. & Raichle, M. E. (1998) The effects of practice on the functional anatomy of task performance. *Proceedings of the National Academy of Sciences USA* 95:853–60. [aSS]
Phillips-Silver, J. & Trainor, L. J. (2005) Feeling the beat: Movement influences infant rhythm perception. *Science* 308:1430. [AJB]

https://doi.org/10.1017/S0140525X08004184 Published online by Cambridge University Press

Piaget, J. (1952) *The origins of intelligence in the child*. International Universities Press. [aSS]
(1953) *The origins of intelligence in the child*, trans. M. Cook. Routledge & Kegan-Paul. (Originally published in French in 1936). [AJB]
(1970) *Genetic epistemology*. Columbia University Press. [aSS]
Plaut, D. C., McClelland, J. L., Seidenberg, M. S. & Patterson, K. (1996) Understanding normal and impaired word reading: Computational principles in quasi-regular domains. *Psychological Review* 103:56–115. [aSS]
Plomin, R. & Dale, P. S. (2000) Genetics and early language development: A U. K. study of twins. In: *Speech and language impairments in children: Causes, characteristics, intervention and outcome*, ed. D. V. M. Bishop & L. B. Leonard, pp. 35–51. Psychology Press. [aSS]
Plomin, R. & Kovacs, Y. (2005) Generalist genes and learning disabilities. *Psychological Bulletin* 131:592–617. [rMSCT]
Plomin, R. & Rutter, M. (1998) Child development, molecular genetics, and what to do with genes once they are found. *Child Development* 69:1221–40. [aSS]
Port, R. & van Gelder, T. (1995) *Mind as motion: Explorations in the dynamics of cognition*. MIT Press. [RMF]
Posner, M. I. (1993) Attention before and during the decade of the brain. In: *Synergies in experimental psychology, artificial intelligence, and cognitive neuroscience: vol. XIV, Attention and performance*, ed. D. Meyers & S. Kornblum, pp. 343–50. MIT Press. [aSS]
Posner, M. I., Petersen, S. E., Fox, P. T. & Raichle, M. E. (1988) Localization of cognitive functions in the human brain. *Science* 240:1627–31. [aSS]
Praag, H. V., Schinder, A. F., Christie, B. R., Toni, N., Palmer, T. D. & Gage, F. H. (2002) Functional neurogenesis in the adult hippocampus. *Nature* 415:1030–34. [rMSCT]
Prechtl, H. F. R. (2001) Prenatal and early postnatal development of human motor behaviour. In: *Handbook of brain and behaviour in human development*, ed. A. F. Kalverboer & A. Gramsbergen, pp. 415–27. Kluwer Academic Press. [aSS]
Pribram, K. H. (1965) Proposal for a structural pragmatism: Some neuropsychological considerations of problems in philosophy. In: *Scientific psychology: Principles and approaches*, ed. B. Worden & E. Nagel, pp. 426–59. Basic Books [KP]
(1974) How is it that sensing so much, we can do so little? In: *Central processing of sensory input*, ed. F. O. Schmitt & F. G. Worden, contributing ed. K. H. Pribram, pp. 249–61. MIT Press. [KP]
(1986) The role of cortico-cortical connections. In: *Two hemispheres, one brain: Functions of the corpus callosum*, ed. F. Lapore, M. Ptito, & H. Jasper, pp. 523–40. Alan Liss. [KP]
(1991) Images of achievement and action spaces: Somatic processes in the control of action. In: *Brain and perception: Holonomy and structure in figural processing*, pp. 121–61. Lawrence Erlbaum Associates. [KP]
(2006) What makes humans humane. *Journal of Biomedical Discovery and Collaboration* 1:14. [KP]
Prigogine (1980) *From being to becoming*. Freeman. [KP]
Prigogine, I. & Stengers, I. (1984) *Order out of chaos*. Bantam. [KP]
Puce, A., Allison, T., Bentin, S., Gore, J. C. & McCarthy, G. (1998) Temporal cortex activation in humans viewing eye and mouth movements. *Journal of Neuroscience* 18:2188–99. [aSS]
Purves, D., Augustine, G. J., Fitzpatrick, D., Katz, L. C., LaMantia, A. S. & McNamara, J. O. (1997) *Neuroscience*. Sinauer. [aSS]
Quartz, S. R. & Sejnowski, T. J. (1997) The neural basis of cognitive development: A constructivist manifesto. *Behavioral and Brain Sciences* 20:537–56. [aSS, rMSCT]
Quinlan, P. T. (1988) Structural change and development in real and artificial neural networks. *Neural Network* 11:577–99. [aSS]
Quinlan, P. T., van der Maas, H. L. J., Jansen, B. R. J., Booij, O. & Rendell, M. (2007) Re-thinking stages of cognitive development: An appraisal of connectionist models of the balance scale task. *Cognition* 103:413–59. [TRS]
Rabbitt, P. (1997) *Methodology of frontal and executive function.* Psychology Press. [JF]
Rainer, G. & Miller, E. K. (2000) Effects of visual experience on the representation of objects in the prefrontal cortex. *Neuron* 27:179–89. [aSS]
Rakic, P. (1988) Specification of cerebral cortical areas. *Science* 241:170–76. [aSS]
Ramus, F. (2004) Should neuroconstructivism guide developmental research? *Trends in Cognitive Sciences* 8(3):100–101. [rMSCT]
Rao, S. C., Rainer, G. & Miller, E. (1997) Integration of "what" and "where" in the primate prefrontal cortex. *Science* 276:821–24. [aSS]
Regier, T. (1996) *The human semantic potential*. MIT Press. [RMF, rMSCT]
Richardson, F. & Thomas, M. S. C. (2008) Critical periods and catastrophic interference effects in the development of self-organizing feature maps. *Developmental Science* 11(3):371–89. [rMSCT]
Rivière, A. (2003) Desarrollo y educación: El papel de la educación en el "diseño" del desarrollo humano. In: *Ángel Rivière: Obras Escogidas. Volumen III. Metarrepresentación y Semiosis*, ed. M. Belinchón, A. Rosa, M. Sotillo & I. Marichalar, pp. 203–42. Panamericana. [RC]
Robertson, S. S. (1988) Mechanism and function of cyclicity in spontaneous movement. In: *Behavior of the fetus*, ed. W. P. Smotherman & S. R. Robinson, pp. 77–94. Telford. [aSS]
Robertson, S. S., Bacher, L. F. & Huntington, N. J. (2001) The integration of body movement and attention in young infants. *Psychological Science* 12:523–26. [aSS]
Robertson, S. S., Guckenheimer, J., Masnick, A. M. & Bacher, L. F. (2004) The dynamics of infant visual foraging. *Developmental Science* 7:194–200. [aSS]
Rogers, T. T. & McClelland, J. L. (2004) *Semantic cognition: A parallel distributed processing approach*. MIT Press. [rMSCT]
Rogoff, B. (1998) Cognition as a collaborative process. In: *Handbook of child psychology: Cognition, perception and language*, ed. W. Damon, pp. 679–744. Wiley. [aSS]
(1990) *Apprenticeship in thinking, cognitive development in social contexts.* Oxford University Press. [aSS]
(2003) *The cultural nature of human development*. Oxford University Press. [aSS]
Rosenzweig, M. R. (1996) Aspects of the search for neural mechanisms of memory. *Annual Review of Psychology* 47:1–32. [rMSCT]
Rutter, M. (2007) Gene-environment interdependence. *Developmental Science* 10:12–18. [rMSCT]
Schlesinger, M. (2004) Evolving agents as a metaphor for the developing child. *Developmental Science* 7:154–68. [aSS]
Seidenberg, M. S. & McClelland, J. L. (1989) A distributed, developmental model of word recognition and naming. *Psychological Review* 96:523–68. [aSS]
Shaywitz, B. A. & Shaywitz, S. E. (1994) Learning disabilities and attention disorders. In: *Principles of pediatric neurology*, ed. K. Swaiman, pp. 1119–51. Mosby. [aSS]
Sheridan, S. R. (1997) *Drawing/Writing and the new literacy*. Drawing/Writing Publications. [aSS]
Shrager, J. & Johnson, M. H. (1996) Dynamic plasticity influences the emergence of function in a simple cortical array. *Neural Networks* 9:1119–29. [aSS]
Shultz, T. R. (2003) *Computational developmental psychology*. MIT Press. [aSS, TRS]
Shultz, T. R., Mysore, S. P. & Quartz, S. R. (2007a) Why let networks grow? In: *Neuroconstructivism, Vol. 2: Perspectives and prospects*, ed. D. Mareschal, S. Sirois, G. Westermann & M. H. Johnson, pp. 65–98. Oxford University Press. [TRS]
Shultz, T. R., Rivest, F., Egri, L., Thivierge, J.-P. & Dandurand, F. (2007b) Could knowledge-based neural learning be useful in developmental robotics? The case of KBCC. *International Journal of Humanoid Robotics* 4:245–79. [TRS]
Shultz, T. R. & Rivest, F. (2001) Knowledge-based cascade-correlation: Using knowledge to speed learning. *Connection Science* 13:1–30. [TRS]
Siegler, R. S. & Klahr, D. (1982) When do children learn? The relationship between existing knowledge and the acquisition of new knowledge. In: *Advances in instructional psychology*, ed. R. Glazer, pp. 121–211. Erlbaum. [TRS]
Sieratzki, J. S. & Woll, B. (1998) Toddling into language: precocious language development in motor-impaired children with spinal muscular atrophy. In: *Proceedings of the 22nd Annual Boston University Conference on Language Development, Volume 2*, ed. A. Greenhill, M. Hughes, H. Littlefield & H. Walsh, pp. 684–94. Cascadilla Press. [aSS]
Simon, T. J., Hespos, S. J. & Rochat, P. (1995) Do infants understand simple arithmetic? A replication of Wynn (1992). *Cognitive Development* 10253–69. [aSS]
Sirois, S. (2004) Autoassociator networks and insights into infancy. *Developmental Science* 7:133–40. [aSS]
(2005) Hebbian motor control in a robot-embedded model of habituation, *Proceedings of the International Joint Conference on Neural Networks (IJCNN 2005)* 2772–77: IEEE. [aSS]
Sirois, S. & Mareschal, D. (2002) Models of infant habituation. *Trends in Cognitive Sciences* 6:293–98. [aSS]
(2004) An interacting systems model of infant habituation. *Journal of Cognitive Neuroscience*, 16:1352–62. [aSS, rMSCT]
Slater, A., Morison, V., Somers, M., Mattock, A., Brown, E. & Taylor, D. (1990) Newborn and older infants' perception of partly occluded objects. *Infant Behavior and Development* 13:33–49. [aSS]
Sloutsky, V. M., Lo, Y.-F. & Fisher, A. (2001) How much does a shared name make things similar? Linguistic labels, similarity and the development of inductive inference. *Child Development* 72:1695–709. [aSS]
Smith, L. B. & Thelen, E. (1993) *A dynamic systems approach to development*. MIT Press. [RMF]
Sokolov, E. N. (1963) *Perception and the conditioned reflex*. Pergamon. [aSS]

https://doi.org/10.1017/S0140525X08004184 Published online by Cambridge University Press

Sokolov, E. N. & Vinogradova, O. S. (1975) *Neuronal mechanisms of the orienting reflex*. Erlbaum. [aSS]
Sotillo, M., García Nogales, M. A. & Campos, R. (2007) Teoría de la mente y lenguaje: El caso del síndrome de Williams. *Infancia y Aprendizaje* 30(3):459–74. [RC]
Spear, L. P. (2000) The adolescent brain and age-related behavioral manifestations. *Neuroscience and Biobehavioral Reviews* 24:417–63. [JF]
Spelke, E. S., Breinlinger, K., Macomber, J. & Jacobson, K. (1992) Origins of knowledge. *Psychological Review* 99:605–32. [aSS]
Sporns, O. (2007) What neuro-robotic models can teach us about neural and cognitive development. In: *Neuroconstructivism: perspectives and prospects, Volume II*, ed. D. Mareschal, S. Sirois, G. Westermann & M. H. Johnson, pp. 179–204. Oxford University Press. [RL, rMSCT]
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. [aSS]
Stager, C. L. & Werker, J. F. (1997) Infants listen for more phonetic detail in speech perception tasks than in word-learning tasks. *Nature* 388:381–82. [aSS]
Stein, J. & Walsh, V. (1997) To see but not to read: The magnocellular theory of dyslexia. *Trends in Neurosciences* 20:147–52. [aSS]
Stern, Y. (2002) What is cognitive reserve? *Journal of the International Neuropsychological Society* 8:448–60. [rMSCT]
Tager-Flusberg, H. & Sullivan, K. (2000) A componential view of theory of mind: Evidence from Williams syndrome. *Cognition* 76(1):59–89. [RC]
Thatcher, R. W. (1992) Cyclic cortical reorganization during early childhood. Special Issue: The role of frontal lobe maturation in cognitive and social development. *Brain and Cognition* 20:24–50. [rMSCT]
Thelen, E., Corbetta, D. & Spencer, J. P. (1996) Development of reaching during the first year: Role of movement speed. *Journal of Experimental Psychology: Human Perception and Performance* 22:1059–76. [aSS]
Thelen, E. & Smith, L. B. (1994) *A dynamic systems approach to the development of cognition and action*. MIT Press. [BK, aSS]
Thomas, M. S. C. (2004) From scientific research to intervention in Williams syndrome. *The Williams Syndrome Foundation UK Magazine* 51(Summer):28–31. [rMSCT]
Thomas, M. S. C. & Johnson, M. H. (2006) The computational modeling of sensitive periods. *Developmental Psychobiology* 48(4):337–44. [rMSCT]
(2008) New advances in understanding sensitive periods in brain development. *Current Directions in Psychological Science* 17(1):1–5. [rMSCT]
Thomas, M. S. C. & Karmiloff-Smith, A. (2002) Are developmental disorders like cases of adult brain damage? Implications from connectionist modeling. *Behavioral and Brain Sciences* 25(6):727–88. [rMSCT]
(2003) Modelling language acquisition in atypical phenotypes. *Psychological Review* 110:647–82. [aSS]
Thorpe, W. H. (1956) *Learning and instinct in animals*. Methuen. [aSS]
Trehub, S. (1976) The discrimination of foreign speech contrasts by infants and adults. *Child Development* 47:466–72. [aSS]
Triesch, J., Teuscher, C., Deák, G. & Carlson, E. (2006) Gaze following: Why (not) learn it? *Developmental Science* 9:125–47. [aSS]
Tucker, D. M. (2007) *Mind from body: Experience from neural structure*. Oxford University Press. [RL]
Turrigiano, G., Abbott, L. F. & Marder, E. (1994) Activity-dependent changes in the intrinsic properties of cultured neurons. *Science* 264:974–77. [aSS]
Ungerleider, L., Ganz, L. & Pribram, K. H. (1977) Size constancy in the rhesus monkeys: Effects of pulvinar, prestriate, and inferotemporal lesions. *Experimental Brain Research* 27:251–69. [KP]
Ungerleider, L. G. & Mishkin, M. (1982) Two cortical visual systems. In: *Analysis of visual behavior*, ed. D. J. Ingle, M. A. Goodale & R. J. W. Mansfield, pp. 549–86. MIT Press. [aSS]
Valenza, E., Simion, F., Cassia, V. M. & Umilta, C. (1996) Face preference at birth. *Journal of Experimental Psychology: Human Perception and Performance* 22:892–903. [aSS]
Van der Lely, H. K. J. (1997) Language and cognitive development in a grammatical SLI boy: Modularity and innateness. *Journal of Neurolinguistics* 10:75–107. [aSS]
Van der Meer, A. L. H., Van der Weel, F. R. & Lee, D. N. (1995) The functional significance of arm movements in neonates. *Science* 267:693–95. [aSS]
Van Essen, D. C., Anderson, C. H. & Felleman, D. J. (1992) Information processing in the primate visual system: An integrated systems perspective. *Science* 255:419–23. [aSS]
Vargha-Khadem, F., Gadian, D. G., Copp, A. & Mishkin, M. (2005) FOXP2 and the neuroanatomy of speech and language. *Nature Reviews Neuroscience* 6(2):131–38. [rMSCT]
Vihman, M. M. (1991) Ontogeny of phonetic gestures. In: *Modularity and the motor theory of speech perception*, ed. I. Mattingly & M. Studdert-Kennedy, pp. 69–84. Erlbaum. [aSS]
(2002) The role of mirror neurons in the ontogeny of speech. In: *Mirror neurons and the evolution of brain and language*, ed. M. Stamenov & V. Gallese, pp. 305–14. John Benjamins. [aSS]
von Hofsten, C. (2004) An action perspective on motor development. *Trends in Cognitive Sciences* 8:266–72. [AJB]
Vygotsky, L. (1986) *Thought and language*. MIT Press. [aSS]
Vygotsky, L. S. (1978) *Mind in Society. The developmental of higher psychological processes*. Harvard University Press. [aSS]
Waddington, C. H. (1953) Genetic assimilation of an acquired character. *Evolution* 7:118–26. [aSS]
(1957) *The strategy of the genes*. Allen and Unwin. [aSS]
Wallace, V., Menn, L. & Yoshinaga-Itano, C. (1998) Is babble the gateway to speech for all children? A longitudinal study of children who are deaf or hard of hearing. *Volta Review* 100:121–48. [aSS]
Walsh, V., Ashbridge, E. & Cowey, A. (1998) Cortical plasticity in perceptual learning demonstrated by transcranial magnetic stimulation. *Neuropsychologia* 36:363–67. [aSS]
Watkins, K. E., Dronkers, N. F. & Vargha-Khadem, F. (2002a) Behavioural analysis of an inherited speech and language disorder: Comparison with acquired aphasia. *Brain* 125:452–64. [aSS]
Watkins, K. E., Vargha-Khadem, F., Ashburner, J., Passingham, R. E., Connelly, A., Friston, K. J., Frackowiak, R. S. J., Mishkin, M. & Gadian, D. G. (2002b) MRI analysis of an inherited speech and language disorder: Structural brain abnormalities. *Brain* 125:465–78. [aSS]
Webb, B. (1994) Robotic experiments in cricket phonotaxis. In: *From animals to animats 3: Proceedings of the Third International Conference on the Simulation of Adaptive Behaviour Brighton*, ed. D. Cliff, P. Husbands, J.-A. Meyer & S. W. Wilson, pp. 45–54. MIT Press. [aSS]
Werker, J. & Tees, R. (1984) Cross-language speech perception: Evidence for perceptual reorganization during the first year of life. *Infant Behavior and Development* 7:49–63. [aSS]
Westermann, G. (2001) A model of perceptual change by domain integration. In: *Proceedings of the 23rd Annual Conference of the Cognitive Science Society*, ed. J. D. Moore & K. Stenning, pp. 1100–105. Erlbaum. [rMSCT]
Westermann, G., Mareschal, D., Johnson, M. H., Sirois, S., Spratling, M. W. & Thomas, M. S. C. (2007) Neuroconstructivism. *Developmental Science* 10(1):75–83. [rMSCT]
Westermann, G. & Miranda, E. R. (2004) A new model of sensorimotor coupling in the development of speech. *Brain and Language* 89:393–400. [aSS]
Westermann, G., Sirois, S., Shultz, T. & Mareschal, D. (2006) Modeling developmental cognitive neuroscience. *Trends in Cognitive Sciences* 10:227–33. [AJB]
Wiesel, T. N. (1982) Postnatal development of the visual cortex and the influence of environment. *Nature* 299:583–91. [GMI]
Wilcox, T. (1999) Object individuation: Infants' use of shape, size, pattern, and color. *Cognition* 72:125–66. [aSS]
Wilcox, T. & Schweinle, A. (2002) Object individuation and event mapping: Developmental changes in infants' use of featural information. *Developmental Science* 5:132–50. [aSS]
Wilson, E. O. (1976) Author's reply to multiple review of "Sociobiology." *Animal Behaviour* 24:716–18. [PB]
Wisniewski, E. J. (1995) Prior knowledge and functionally relevant features in concept learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 21:449–68. [TRS]
Xu, F. & Carey, S. (1996) Infants' metaphysics: The case of numerical identity. *Cognitive Psychology* 30:111–53. [aSS]
Zeki, S. (1983) Color coding in the prestriate cortex: the response of wave-length selective and color coded cells in the monkey to changes in wave length composition. *Neuroscience* 9:741–65. [KP]
Zelazo, P. R., Weiss, M. J. S. & Tarquinio, N. (1991) Habituation and recovery of neonatal orienting to auditory stimuli. In: *Newborn attention: Biological constraints and the influence of experience*, ed. M. J. S. Weiss & P. R. Zelazo, pp. 120–41. Ablex. [aSS]
Zufferey, P. D., Jin, F., Nakamura, H., Tettoni, L. & Innocenti, G. M. (1999) The role of pattern vision in the development of cortico-cortical connections. *European Journal of Neuroscience* 11:2669–88. [GMI]

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