

# The constructivist brain

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**How do the representations underlying cognitive skills emerge? It is becoming increasingly apparent that answering this question requires integration of neural, cognitive and computational perspectives. Results from this integrative approach resonate with Piaget's central constructivist themes, thus converging on a 'neural constructivist' approach to development, which itself rests on two major research developments. First, accumulating neural evidence for developmental plasticity makes nativist proposals increasingly untenable. Instead, the evidence suggests that cortical development involves the progressive elaboration of neural circuits in which experience-dependent neural growth mechanisms act alongside intrinsic developmental processes to construct the representations underlying mature skills. Second, new research involving constructivist neural networks is elucidating the dynamic interaction between environmentally derived neural activity and developmental mechanisms. Recent neurodevelopmental studies further accord with Piaget's themes, supporting the view of human cortical development as a protracted period of hierarchical-representation construction. Combining constructive growth algorithms with the hierarchical construction of cortical regions suggests that cortical development involves a cascade of increasingly complex representations. Thus, protracted cortical development, while occurring at the expense of increased vulnerability and parental investment, appears to be a powerful and flexible strategy for constructing the representations underlying cognition.**

Developmental researchers still struggle with a paradox first proposed by Plato, who argued that learning is impossible except against a rich stock of prior knowledge. Indeed, so rich did this prior knowledge have to be that it reduced learning to little more than recollection. By quantifying this innate knowledge as inductive bias, decades of work in formal learning theory reinforced this paradox: learning is too hard without first severely restricting what can be learned<sup>1</sup>. Unconstrained, or *tabula rasa*, learning is infeasible. This suggests that the major hurdle in acquiring cognitive skills is not one involving statistical inference *per se*. Rather, it is the prior issue of the source of appropriate representations that make learning possible at all<sup>2</sup>.

Faced with these limitations on learning, Chomsky<sup>3</sup>, Fodor<sup>4</sup>, and other nativists presented influential arguments for why a substantial amount of symbolic knowledge must be encoded *a priori* in cortical structures known as cognitive modules or mental organs. Although Chomsky remained uncommitted to an evolutionary origin of mental modules, today this nativist model is the cornerstone of evolutionary psychology's proposals regarding how evolutionary pressures might have shaped the human mind as a collection of domain-specific mental modules<sup>5</sup>.

As powerful as nativist arguments were, accumulating evidence from developmental neurobiology and molecular genetics makes it increasingly problematic to suppose that

complex symbolic knowledge is somehow encoded in the cortex prior to experience (see Box 1 and Refs 6–8). This emerging evidence for developmental plasticity appears to result in a paradox: whereas learning-theoretic considerations strongly suggest that learning is feasible only when highly constrained, neurobiology suggests a much less developmentally constrained cortex than previously supposed. A major challenge facing theories of development today, then, lies in reconciling the learning-theoretic constraints against *tabula rasa* learning with the accumulating evidence for developmental plasticity.

Recently, a new approach to these questions has emerged, as advances in developmental neurobiology, developmental psychology, and neural computation are integrated into an approach known as developmental cognitive neuroscience<sup>9</sup>. This differs from many previous approaches in its explicit focus on characterizing the process of developmental change from both functional and structural perspectives<sup>10</sup>. In this review, I will examine the converging lines of evidence from cognitive, neural and neural computational perspectives that support a neural constructivist approach to development. Although Piaget's developmental themes<sup>11</sup> were dismissed by nativists as theoretically confused<sup>12</sup>, I will highlight where this emerging view supports Piaget's original developmental proposals regarding the hierarchical, activity-mediated construction of mental representations.

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## Box 1. Cortical pre-specification: evolutionary and developmental considerations

During the last ten years, considerable evidence has accumulated regarding cortical developmental plasticity. For example, cortical transplants (Ref. a), rerouting projections to novel targets (Ref. b), and clonal analysis of cell migration (Ref. c) all suggest that the regional characteristics of mature cortex depend on interaction with afferent input (Ref. d). Although this view is based mainly on non-human studies, recent imaging studies of human cortical developmental plasticity in subjects who were blind from an early age support this view (Refs e,f). In particular, these studies suggest that the tactile processing pathways usually linked to the secondary somatosensory area are rerouted in blind subjects to the ventral occipital cortical regions originally reserved for visual shape discrimination. Therefore, in blind subjects cortical areas normally underlying vision may be recruited for other sensory modalities. This finding is supported by the disruption of Braille discrimination tasks using transcranial magnetic stimulation of occipital cortex in blind subjects (Ref. g). While these results do not preclude domain-specific biases in various cortical regions, the capacity of cortical regions to become functional within a novel sensory domain makes it problematic to posit native complex sensory encodings in them.

Consistent with these results on cortical developmental plasticity, O'Leary (Refs h,i) refers to the immature cortex as protocortex, which shares a common basic circuitry and repetitive arrays of cell types, but which requires afferent input, both intrinsically generated and environmentally derived, for its regional specialization. The protracted postnatal development of human cortex discussed in this review suggests that it maximizes the capacity of environmentally-derived patterns of neural activity to influence the structure and function of some cortical regions.

Recent comparative work, evolutionary analyses, and investigation of the molecular genetics of development further suggest that phylogenetic differences in the size, function and pattern of connectivity of cortical areas are not locally determined. Rather, many aspects of brain complexity appear to originate as systemic, cascading effects that derive from prolongation of fetal brain growth. In an important comparative study (Ref. j), the size of brain components was found to be highly predictable from absolute brain size by a nonlinear function. The study also found that the order of neurogenesis is highly conserved across a wide range of mammals and correlates with the relative enlargement of structures as brain size increases, with disproportionately large growth occurring in late-generated structures. Given this conservation, the most likely brain alteration resulting from selection for any behavioral ability may be a coordinated enlargement of the entire nonolfactory brain. Therefore, alterations in both the relative size of brain components and overall brain size may derive from heterochronic changes in

fetal brain growth, that is, changes involving the relative timing of developmental events. Prolongation of fetal brain growth may in turn derive from changes in segmentation in very early embryonic development (Ref. k). If so, then changes in homeotic gene expression altering the initial production of late-maturing embryonic stem neurons, a heterochronic event known as predisplacement, may underlie key facets of human brain evolution (Ref. l). These highly linked regularities in the development and evolution of mammalian brains make evolutionary proposals that depend on region-specific, modular adaptations problematic. Rather, it suggests the evolution of robust, flexible developmental strategies (Ref. m) in which the determination of mature function in the cortex depends heavily on epigenetic mechanisms, including progressive specialization by afferent input through constructive development.

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### Selectionist development

The best-known attempts to integrate cognitive and neural perspectives on development are the neural selectionist theories of Changeux and colleagues<sup>13</sup> and Edelman<sup>14</sup>. Although there is considerable disagreement concerning the core features of neural selectionism<sup>10</sup>, according to its most widely adopted (Darwinian) interpretation, development essentially involves two phases. The first phase is an initial activity-independent overproduction of cortical structures,

followed by a second phase characterized by an activity-dependent selection of a subset of that structure. According to this view, cognitive representations have their origin in an epigenetic process, one combining both genetic and intrinsically generated signals, whose function is to create a diversity of representations, analogous to antibody production in the immune system. This produces the background knowledge against which learning proceeds. Cognitive development then corresponds to a competitive search through

## Box 2. Selection and construction in the development of the visual system

One of the most widely cited model systems believed to support the overproduction/pruning model is the development of the visual system, and, in particular, the development of ocular dominance columns. Ocular dominance (OD) columns are alternating, anatomically defined regions of input from primarily one eye. According to a widespread account, OD development involves an initial period of axonal overproduction, in which arbors overlap, followed by a period of segregation mediated by selective axonal pruning. Although an important early study (Ref. a) contains a pair of Golgi-stained cells at early and late developmental stages that are often cited as evidence for selectionism, subsequent studies of individual geniculocortical arbors confirm both the retraction of early axonal structure in inappropriate regions and selective growth within appropriate target sites, the net result being a progressive increase in structural complexity (Ref. b). As Antonini and Stryker demonstrated (Ref. b), during the first week of segregation between left and right eye input, axonal branch point numbers increased from a median value of 34.5 to 96.0, while total arbor length increased from 7538 to 12848 microns. Similarly, the area an arbor occupied also increased during this time, becoming significant by postnatal day 39. Even this is still about half the coverage area of the mature axonal arbor (Ref. c). In a recent review of the development of the visual pathway, Katz and Shatz (Ref. d) conclude, 'the strategy for forming adult circuits involves a local control of sprouting and synaptogenesis rather than selection from a large pre-existing repertoire' (p. 1134).

While this more constructivist account holds for projections to visual cortex, approximately 90% of synapses in cortex originate from other cortical neurons. Among these, pyramidal cells in layers 2/3 have long, intrinsic horizontal axon collaterals within both layer 2/3 and layer 5, which form periodic 'clusters' of finer axon branches. The development of this system also appears to involve a progressive increase in structural complexity. In a recent review, Katz (Ref. e) concludes, 'this "constructionist" view of the role of activity (Purves, 1988) seems to more plausibly account for the development of the system of clustered connections than mechanisms based on large-scale regressive events' (p. 534).

The presence of constructive development in these model systems suggests a more balanced role for regressive events. Rather than exhausting activity-dependent developmental mechanisms, regressive events act alongside constructive ones as the sort of error-correction that any reduced view of neural specificity must include (see Ref. f for an extended discussion of this point). However, the net result appears to be a progressive elaboration of cortical circuits. In this regard, it is interesting to note that recent neural computational models have explored the role of neurotrophic factors in ocular dominance column formation. In this model, axonal process sprouting and retraction are governed by competition for neurotrophic support (Refs g,h). It should also be noted that activity-dependent synaptogenesis underlies some mature forms of plasticity, as is well documented (Ref. i).

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these representations, in which those representations that are poorly matched to the needs of the organism are eliminated. In terms of human development, Huttenlocher's<sup>15</sup> influential study on human cortical synaptogenesis helped make the Darwinian view a popular one. According to this view, human cortical synaptogenesis is completed by the end of the second postnatal year of life. Subsequent to that, development involves a paring down of these exuberant structures lasting into adolescence.

### Constructive neural development

Neural selectionism was offered as an alternative to a proposal that goes back at least to Hebb<sup>16</sup>, who is best known for a neurally based associative learning rule that bears his name. Hebb, however, made his proposal in the developmental context of the construction of cell assemblies. Viewed from that developmental perspective, Hebb's rule

was a proposal for how patterned neural activity could participate in the construction of neural circuits. In recent years, evidence has accumulated to support Hebb's proposal that neural activity, both spontaneously generated and experience-dependent, plays a role in constructing cortical circuits, rather than simply selecting among pre-existing ones. This evidence supports the view that the development of cortical circuits is a 'constructivist' one of progressive elaboration rather than selective elimination, even for model selectionist systems such as vision (see Box 2). Purves et al.<sup>17</sup>, for example, examined the evidence for an initial excess of synaptic numbers, axonal processes, and dendritic processes and concluded that the bulk of the evidence favors progressive increases in these measures during maturation. As Purves et al.<sup>17</sup> conclude, 'we consider a Darwinian [selectionist] framework to be particularly misleading; extrapolation to a general principle from the regression of a small

number of axon collaterals and their synapses in particular cases obscures the overwhelmingly progressive and constructive nature of neural development' (pp. 463–464).

Quartz and Sejnowski<sup>10</sup> also examined the developmental timecourse of synaptic numbers, axonal processes and dendritic arbors and concluded that the bulk of the evidence favors progressive increases in these measures during development. In addition, they reviewed neurobiological results spanning over thirty years that support the role for activity-dependent mechanisms in the progressive construction of neural circuits. In this regard, much recent work has focused on the role of factors regulating neuronal growth and differentiation, particularly neurotrophins, in the activity-dependent development of cortex<sup>18</sup>. Of particular interest is a recent study<sup>19</sup> that demonstrated a requirement for conjoint neurotrophin signaling and activity, which provides a mechanism for enhancing the growth and connectivity of active neurons in developing cortex.

There is emerging evidence, then, that cortical development is not characterized by an early overproduction followed by selective elimination. Nor is it exhausted by mechanisms of selective elimination operating on transient, exuberant structures. This revised view of activity's role in the construction of neural circuits forms the basis for an emerging neural constructivist view, which examines how representational structures are progressively elaborated during development through the interaction of intrinsic developmental programs and activity-dependent growth mechanisms<sup>10,20</sup>. In place of a cortex containing specialized modules, neural constructivism begins with what O'Leary<sup>21</sup> terms 'protocortex', a fairly generic cortical architecture sharing a common basic circuitry and repetitive arrays of cell types, but which requires afferent input, both intrinsically generated and environmentally derived, for its regional specialization (see Box 1). In keeping with Chenn *et al.*'s<sup>21</sup> statement that 'the modality of thalamic input to an individual neocortical area largely determines the functional identity of that area' (p. 462), neural constructivism regards modularization not as the starting point of development, but rather its endpoint, as cortex becomes increasingly specialized through the interaction between afferent input carrying domain-specific information and intrinsic cortical properties<sup>22</sup>. The neural constructivist approach thus attempts to characterize how the representations underlying human cognitive skills emerge through a process of construction acting on a protocortex in which it is infeasible to posit complex symbolic encodings.

#### Spontaneously generated and experience-dependent activity in the construction of cortical circuitry

One clue in understanding how this constructive process may operate lies in the well-established finding that intrinsically generated neural activity plays an important role in the activity-dependent construction of some neural structures<sup>23</sup>. In the visual system, for example, spontaneously generated waves of action potentials are present in the mammalian retina well before the onset of vision<sup>24</sup>. Bursts of action potentials in retinal ganglion cells are correlated among neighboring cells and produce waves of neural activity that spread across restricted regions of the retina<sup>25</sup>. These and other patterns of correlated, spontaneously generated

neural activity are believed to participate in the development of a number of the structural and functional features of visual cortex.

The developmental role of spontaneously generated neural activity suggests the existence of a conserved developmental mechanism that may also underlie the experience-dependent development of neural structures. Indeed, the mammalian visual system is a paradigmatic example of a neural system in which the final steps of constructing its cortical circuits requires experience-dependent neural activity. Therefore, this experience-dependent mode of circuit construction does not require novel mechanisms. Instead, it only requires a shift from spontaneously generated activity to experience-dependent activity with the onset of experience. As Katz and Shatz<sup>23</sup> state, '[T]he sequential combination of spontaneously generated and experience-dependent neural activity endows the brain with an ongoing ability to accommodate to dynamically changing inputs during development and throughout life (p. 1133).' This mode of development, however, is quite different from traditional accounts of neuronal maturation. In particular, because experience-dependent neural activity participates in the postnatal construction of neural circuits, processes traditionally described as learning might cause changes in the very mechanisms of acquisition.

#### *Learning and the activity-dependent construction of neural circuits*

At a general level, the participation of experience-dependent neural activity in the construction of neural circuits may be viewed as a form of learning, not statistical inference *per se*, but one of representation construction. The learning-theoretic considerations alluded to earlier highlight that learning cannot be unconstrained. Instead, learning must always be accomplished relative to some set of representations<sup>2</sup>. This suggested that the central problem of development concerns the origin of these representations. However, since these representations cannot be built into cortex in the form of modules specialized for various domains, the neural constructivist perspective suggests that they are constructed as developmental mechanisms interact with the environment.

Beyond breaking down the traditional distinction between cognitive processes of learning and biological processes of intrinsic maturation, this mode of development, whereby learning plays a role in constructing mental representations, is of course the central theme of Piaget's constructivism. Piaget's attempt to characterize the processes and mechanisms underlying activity-mediated representational change was also arguably the point of failure of his constructivism. Indeed, characterizing change during development has proven to be an enduring challenge<sup>26</sup>. A reason for this is that changes in the structures underlying acquisition alter what can subsequently be learned, adding complex time-dependent properties. A major reaction to Piaget's account and contemporary connectionist ones<sup>7</sup> is the charge that they do not offer a concrete account of representational change<sup>12,27</sup>. As neural constructivist approaches revive this mode of development, they once again raise the challenge of adequately characterizing activity-mediated representation construction.



### Box 3. Neural networks and the learning properties of constructive development

Much neural network research involves networks with fixed architectures. However, a growing body of research focuses on constructive neural networks, in which the architecture itself can be altered as part of learning (Refs a,b). Because the representational properties of neural networks are derived from their structural properties, activity-dependent change in their architecture, whether by the addition of new processing nodes or connections among them, corresponds to a process of representation construction. This provides an important link between the process of representational change and structural development, and so provides a number of insights into the nature of constructive development.

Developmental studies (Refs c,d) using the constructivist neural network method, cascade-correlation (Ref. e), are relevant to understanding the psychological consequences of constructive development. The results on a balance-scale experiment are particularly intriguing. In a balance-scale task, a child is asked to predict the outcome of placing various numbers of equal weights at various distances to the left or right of a fulcrum. Between the ages of four and twelve, children appear to pass through four well-defined, discrete stages determined by sequences of rules as they master this task (Ref. f). The cascade-correlation networks provided better fits to human data than did previous rule-based and connectionist models (Ref. c). In particular, the model displayed two kinds of change, both of which are thought to be central to development. That is, the model displayed quantitative changes as incremental improvement, which was likely mediated by weight changes. However, the model also displayed instances of qualitative restructuring by progressing through the discrete stages children pass through as they master this task. In particular, the emergence of discontinuous, stage-like behavior was mediated by the addition of new units, which expanded the representational capacities of the network. Although the nonlinear dynamics of fixed architectures can also produce discontinuous changes (Ref. g), constructivist neural-network modeling demonstrates how such changes may be mediated by the documented progressive growth of neural circuits. Such expanding, activity-driven ca-

pacities allow for qualitatively novel behaviors by qualitatively shifting performance from one stage to the next, a theme that recurs throughout the developmental literature (Ref. h).

Constructivist modeling also demonstrates that there are many advantages with starting with a limited architecture. Such a network must pass through a phase of limited representational power during early exposure to some problem and then build successively more powerful representational structures. While traditional accounts suggested this weakened a learning system, a general lesson that is emerging from neural network studies of development is that the simplicity of the immature system may be highly beneficial for learning the solutions for complex problems (Refs i,j).

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Neural network research is proving useful in characterizing this process of activity-mediated representation construction (see Box 3 and Ref. 28). In particular, constructive neural networks are ones in which the architecture itself can be altered as part of learning. Since the representational properties of neural networks are derived from their structural properties, activity-dependent change in their architecture, whether by the addition of new processing nodes or connections among them, corresponds to a process of representation construction. Making this link between processes of learning and structural alterations in a developing system is one of the most promising features of neural network modeling.

In particular, neural network studies demonstrate that the acquisition properties of constructivist systems differ from selectionist and nativist views in several key respects<sup>29</sup>. Both the selectionist and nativist approaches are models of selective induction. That is, both characterize acquisition as a search through a pre-defined space of representations in which the target state is embedded. Experience does not

play a role in the construction of these representations, but only in their elimination. For this reason, the selectionist view is reminiscent of some nativist models, as indeed some linguists have adopted the selectionist model for parameter setting models of language acquisition<sup>10,30</sup>. The constructivist approach, in contrast, does not involve a search through a pre-defined hypothesis space, and so it is not one of selective induction – also known as model-based estimation, or parametric regression. Instead, constructivist development builds its representations as it learns, and is thus a form of non-parametric regression.

With constructive neural networks, the structure of the problem domain plays a role in determining the connectivity of the network through experience. Because the construction of the learner's hypothesis space is sensitive to the problem domain facing the learner, this is a way of tailoring the hypothesis space to suit the demands of the problem at hand. Of course, such an approach cannot be unconstrained. Also, activity-dependent constructive processes

modulate intrinsic developmental programs, rather than underlying all growth. Therefore, a major challenge in understanding how the representations underlying cognitive skills emerge is to determine how the emergence of functional cortical maturity is constrained by such features as a generic initial cortical circuitry, conduction velocities, subcortical organization, learning rates, and other factors such as intrinsic behavioral systems that direct the developing system towards certain classes of stimuli<sup>31</sup>.

A recent study in the owl<sup>32</sup> highlights the role of early experience as a constructor of the representations that facilitate learning later in life. The optic tectum of barn owls contains a multimodal map of space. In particular, auditory–visual neurons in the optic tectum associate values of auditory spatial cues with locations in the visual field. This association is accomplished through matching the tuning of tectal neurons for interaural time differences with their visual receptive fields. During development, but not adulthood, there is considerable plasticity in this system, allowing for a wide range of associations to be learned. When juvenile animals were fitted with goggles that shift the visual field, the resulting abnormal associations were learned. Knudsen demonstrated that the range of associations adult owls could learn is greatly expanded in those animals that had learned abnormal associations during development. Although the neural processes underlying this capacity are yet to be fully elucidated, prism experience has been shown to induce changes in patterns of axonal projections that can account for the shift in interaural time difference tuning<sup>33</sup>, thus suggesting that experience can cause the formation of anatomical projections<sup>32</sup>.

From a computational perspective, this intriguing study of the role of early experience in constructing the representations that facilitate later learning highlights the importance of separating learning into distinct problems: learning as statistical inference and as the construction of an efficient set of representations that make statistical inference possible at all. From this perspective, it is striking that one of the most salient properties of human cortical development is its protractedness. The rate of human cortical development appears not to be reduced as compared to non-human primates, a developmental hypothesis known as juvenilization. Rather, human cortical development appears to be far more protracted than in non-human primates. For comparison, the human brain reaches about 90% of its final mass by around five years of age, whereas this landmark appears to be reached in the chimpanzee by two years of age. The extensive postnatal period of human cortical development thus suggests it is particularly malleable to experience-dependent neural activity in the construction of cortical circuits. Combined with learning-theoretic considerations, this strategy appears to be a highly flexible one for creating the representations underlying cognitive skills. To assess the full implications of this developmental mode, however, it is necessary to consider the pattern of human cortical development throughout the brain.

#### Hierarchical constructive development

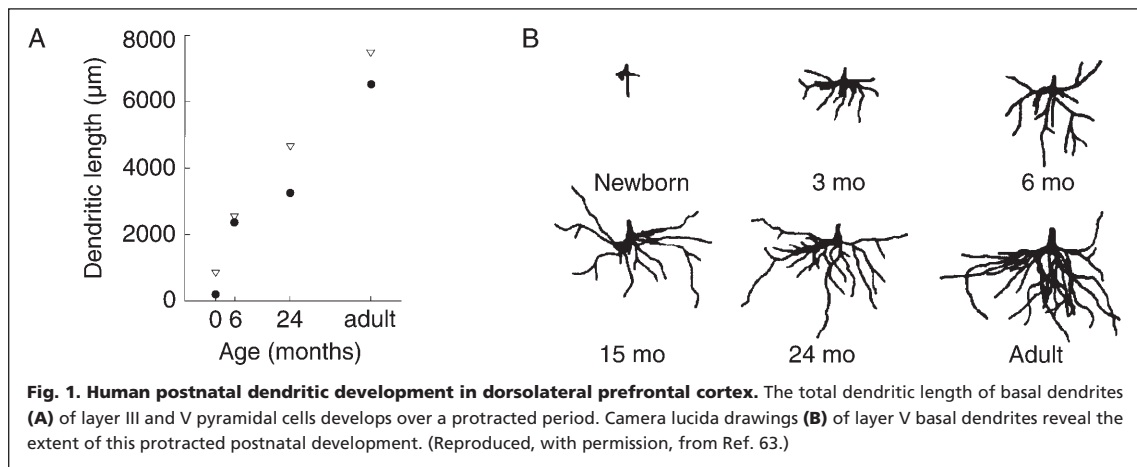
Although many features of Piaget's developmental view have come under extensive criticism, the core idea that de-

velopment involves the expansion of hierarchically organized sequential operations, beginning with perceptual and sensorimotor functions and becoming more combinatorially complex, remains popular<sup>34,35</sup>. Although constructivist neural network models demonstrate how qualitative restructuring can occur in a single network, the brain is a system of such networks, often widely distributed over many regions. It is thus important to consider whether cortical regions develop according to the same schedule, or whether they develop regionally. If the latter, then it would lend support to the view of development as a cascade of increasingly complex representational structures, in which construction in some regions depends on the prior development of others. This would add substantially to the complexity of representational structures that can be constructed through the interaction of intrinsic developmental programs and activity-mediated growth algorithms.

Central to the selectionist model was the notion that the early, exuberant proliferation of synapses occurred simultaneously across the cortex. Known as concurrent synaptogenesis, this influential view was based on electron microscopic studies of synaptogenesis in the rhesus monkey<sup>36,37</sup>. This view suggested that the entire cerebral cortex develops as a whole and that the establishment of cell-to-cell communication may be orchestrated by a single genetic or humoral signal. As Rackic *et al.*<sup>36</sup> pointed out, this view ruled out a hierarchical view of cortical development, that is a developmental ordering from the sensory periphery to higher associational areas. It also suggested that synaptogenesis proceeds according to a different developmental schedule than does myelination and dendritic arborization, both of which develop regionally.

In a more recent study<sup>37</sup> of synaptogenesis in prefrontal cortex (PFC) of rhesus monkey, Bourgeois *et al.* conclude, 'concurrent recruitment of synapses with that of sensory and motor areas supports the concept that the initial establishment of cortical circuitry is governed by general mechanisms common to all areas, independent of their specific functional domain' (p. 78). Even quite recently, synaptogenesis in human PFC was thought to be concurrent with other regions<sup>38</sup>. A recent study of human cortical development in auditory cortex and prefrontal gyrus<sup>39</sup>, however, suggests that concurrent synaptogenesis is not a feature of human cortical development. According to this important finding, human cortical synaptogenesis occurs regionally and in accord with the hierarchical developmental schedule observed for axonal growth, dendritic growth, and myelination of the subcortical white matter<sup>39</sup>. Assimilating the developmental schedule for these various measures, it appears that primary sensory and motor cortical areas are both closer to their mature measures at birth and reach those measures earlier than do areas of association in temporal and parietal regions, and PFC<sup>38</sup>.

This regional pattern of cortical development, proceeding from the sensory periphery to higher association areas, is particularly intriguing given that cortical representations are arranged hierarchically in a way that matches this regional hierarchy. According to Fuster<sup>40</sup>, 'the cortical substrate of memory, and of knowledge in general, can be viewed as the upward expansion of a hierarchy of neural structures' (p. 451).



Although the existence of extensive feedback connections suggests that the notion of a strict hierarchy must be qualified, cortical areas closer to the sensory periphery encode lower-order, or more elementary, representations than do areas further removed, which involve more distributed networks lacking the topographical organization of lower areas. All three sensory modalities – vision, touch and audition – involve what Fuster<sup>40</sup> refers to as a ‘hierarchical stacking of perceptual memory categories in progressively higher and more widely distributed networks’ (p. 455). All three modalities then converge on polysensory association cortex and the limbic structures of the temporal lobe, particularly the hippocampus. This hierarchical organization of representations combined with its hierarchical developmental pattern lends support to the view of development as a cascade of increasingly complex representational structures, in which construction in some regions depends on the prior development of others.

#### *Hierarchical constructive development and prefrontal cortex*

This regional, hierarchical mode of development is particularly intriguing for the development of cognitive functions involving PFC, which are widely thought to underlie much of the uniqueness of human cognitive capacities. PFC appears involved in such capacities as the temporal organization of action<sup>38</sup>, working memory<sup>41</sup>, response learning<sup>42</sup>, and inferential reasoning involving theory of mind<sup>43</sup>. Lesions involving PFC yield a constellation of neuropsychological deficits described variously as difficulties involving planning, concept formation, abstract thinking, decision making, cognitive flexibility, temporal ordering of events, and self-monitoring<sup>44</sup>.

According to one estimate, the relative size of the prefrontal area in modern humans is 202% of the size predicted for an anthropoid ape of our body size. The relative enlargement of PFC in comparison to many other brain regions is widely believed to underlie fundamental components of human cognition. A recent MRI study<sup>45</sup>, however, reports that the relative size of the frontal lobe is similar across hominoids and that humans do not have a larger frontal lobe than expected from a primate brain of the human size. It is possible that these two observations are consistent, however. According to Deacon<sup>46</sup>, the size of regions in the frontal cortex with relatively direct peripheral

links may be constrained by the size of their sources or targets, which are proportional to body size. Because the human body is about three times smaller than predicted for an anthropoid ape of our body size, it might be expected that those regions with more direct peripheral links have not expanded, or may actually be smaller than predicted for an anthropoid ape of our body size. In support of this possibility, Deacon reports that motor cortex is 35% of its predicted size whereas premotor area is about 77% of its predicted size. Because prefrontal cortex lacks direct peripheral connections, it may be less constrained in terms of size.

These observations are consistent with studies indicating that for non-synaptic measures (synaptic measures are not available) frontal lobe development proceeds in hierarchical fashion from areas with peripheral links to those further removed, that is, from motor to premotor and then to prefrontal regions<sup>38</sup>. Although good anatomical data are limited, PFC appears to be the latest cortical structure to mature and also to undergo the greatest postnatal development. Using dendritic arborization as a developmental measure, depending on cortical layer, dendrites in human primary visual cortex are between 30 and 50% of total adult lengths at birth and reach mature lengths between four and 18 months of age<sup>47</sup>. In contrast, the basal dendrites of cells in layer III of dorsolateral PFC grow to over 30 times their length at birth and undergo the majority of their growth after two years of age (Fig. 1). Indeed, PFC appears to continue to develop well into the second decade of life<sup>48,49</sup>. Unfortunately, there are relatively few anatomical studies of human PFC development, and so more detailed observations are unavailable. However, from what available data there are, it appears to agree on the delayed cortical maturation of PFC with respect to other regions<sup>39,50,51</sup>.

Although neo-Piagetian approaches have paid considerable attention to the consequences of PFC maturation<sup>52–54</sup>, an influential review<sup>55</sup> argued against a hierarchical view on the basis of concurrent synaptogenesis. Therefore, new evidence for the delayed structural maturation of PFC, and its place in a hierarchical developmental order, raises the important question of how this mode of development may contribute to the developmental emergence of behavioral functions. Recently, the developmental emergence of PFC and executive functions involved in working memory have been investigated<sup>56</sup>. Working memory involves processes

**Table 1. Summary of CANTAB findings for emergence of working memory**

Task	Neural correlates	Variables coded	Results
Motor screening	Corticostriatal circuitry Basal ganglia	Average error Average response latency	4 < 5,6,7,8, adult 4 < 5 = 6 < 7,8, adult
Spatial memory span	Right ventrolateral prefrontal cortex	Length of memory span	4 < 5,6 < 7,8, adult
Spatial working memory	Dorsal/ventral prefrontal cortex Ascending catecholamine systems	Forgetting errors for: 2-item searches 3-item searches 4-item searches 6-item searches 8-item searches Strategy score	All groups equal 4 < 5,6,7,8, adult 4 < 5,6,7 < 8, adult 4,5,6 < 7,8 < adult 5,6,7,8 < adult* 5,6,7 < 8, adult*
Tower of London	Bilateral parietal cortices Left caudate nucleus Left dorsolateral prefrontal	Excess moves to complete: 2-move problems 3-move problems 4-move problems 5-move problems	All groups equal 4 < 5,6,7,8, adult 5,6,7,8 < adult* 5,6,7,8 < adult*
Pattern recognition	Medial temporal lobe	Percent correct responses	4 < 5,6 < 7,8 < adult
Spatial recognition	Medial temporal and parietal lobes right dorsolateral prefrontal cortex	Percent correct responses	4 < 5,6,7 < 8, adult

< = statistically significant performance differences; \* = 4-year-olds excluded. (Modified from Ref. 56.)

that guide behavioral responses towards future goals based on internal representations of current and anticipated environmental cues, often described as a hierarchical complex of abilities<sup>57,58</sup>.

Luciana and Nelson<sup>56</sup> examined the developmental emergence of functions involved in working memory, through the use of the Cambridge Neuropsychological Test Automated Battery (CANTAB), a test designed to dissociate frontal- from temporal-lobe behavioral functions. The development of prefrontally guided working memory systems, which is thought to involve particularly the dorsolateral region of PFC, in four- to eight-year-old children appears to proceed dimensionally, beginning with the refinement of basic perceptual and sensorimotor functions and culminating with the emergence of distributed networks that integrate complex processing demands (Table 1).

Of particular interest is performance on the 'Tower of London' task, which involves spatial planning and behavioral inhibition and activates the parietal lobe bilaterally, the left dorsolateral prefrontal cortex, and left caudate nucleus in the dorsal striatum<sup>59,60</sup>. Performance on the Tower of London task was found to be critically modulated by task difficulty. On easy problems involving two- and three-item moves, the performance of five- to seven-year-olds is indistinguishable from that of adults. However, as the task becomes more difficult, their performance rapidly deteriorates. Eight-year-olds performed better than did five- to seven-year-olds, but their performance on hard versions was below that of adult levels. These results indicate that prefrontal cortex is functional in children, but processing and integrative capacities are below adult levels. As Luciana and Nelson note, this is consistent with other studies, in which

a stage-like emergence of prefrontally guided behaviors is reported<sup>61</sup>.

Luciana and Nelson consider the possibility of synaptic overproduction in prefrontal cortex as a possible neural correlate of this developmental profile. However, the research reviewed here suggests that the prolonged construction of neural circuits in prefrontal cortex may underlie elements of this stage-like developmental profile. Constructivist neural networks further suggest that this stage-like emergence of executive working memory may be mediated by the progressive elaboration of neural circuits in prefrontal cortex. The hierarchical development of prefrontal cortex also suggests that it may functionally emerge as a late outgrowth of earlier established systems, adding an integrative component. In this regard, Luciana and Nelson suggest that children may resemble frontal lobe patients in the sense that those patients often possess the component processes necessary for working memory, such as intact recognition memory, sensory perception and motor skills, but lack the executive functions necessary to organize and integrate these components effectively. They suggest that the functional maturation might thus be the culminating step in this integrative process. Extending this observation, Luciana and Nelson examine other studies of information processing networks<sup>62</sup> to suggest that simple psychomotor behavior may be accomplished via a network involving the globus pallidus, putamen, thalamus, and premotor areas of the frontal lobe. With increasingly complex information processing demands, such as discrimination learning and working memory, the underlying cortical circuitry becomes more extensive, involving discrete areas of the prefrontal cortex in conjunction with various regions including temporal and parietal association cortices,



hippocampus, amygdala, and the dorsal and ventral striatum. Therefore, both the maturation of integrative circuits and maturation within the PFC itself according to a hierarchical ordering may underlie the functional maturation of working memory. Elucidating the developmental emergence of these functions in more detail, however, will require more extensive anatomical knowledge in order to link these functional changes with concomitant structural changes.

### Conclusion

The converging lines of evidence highlighted in this review suggest that human cortical development is a protracted period of hierarchical representation construction. Cortical development appears not to be concurrent, but instead appears to proceed regionally, from primary motor and sensory areas to higher areas of association in temporal, parietal, and frontal lobes<sup>40</sup>. A growing amount of research further suggests that this development involves the progressive elaboration of neural circuits in which experience-dependent neural growth mechanisms act alongside intrinsic developmental processes to construct the representations underlying mature skills. Combining constructive growth algorithms with the hierarchical construction of cortical regions suggests that cortical development involves a cascade of increasingly complex representations. Protracted human cortical development, while coming at the expense of increased vulnerability and parental investment, appears to be both a powerful means of constructing the representations underlying cognition and a flexible strategy for dealing with a dynamic environment. Such experience-dependent neural construction strategies may also underlie the lifespan cortical plasticity that is the hallmark of human cognition. While this approach appears to be a promising beginning by reconciling both learning-theoretic and biological constraints facing developing systems, a major challenge is to elucidate the dynamic interaction between intrinsic brain properties and experience-dependent neural activity in the construction of the neural structures underlying cognition.

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# Ten years of the rational analysis of cognition

Nick Chater and Mike Oaksford

**Rational analysis is an empirical program that attempts to explain the function and purpose of cognitive processes. This article looks back on a decade of research outlining the rational analysis methodology and how the approach relates to other work in cognitive science. We illustrate rational analysis by considering how it has been applied to memory and reasoning. From the perspective of traditional cognitive science, the cognitive system can appear to be a rather arbitrary assortment of mechanisms with equally arbitrary limitations. In contrast, rational analysis views cognition as intricately adapted to its environment and to the problems it faces.**

In 1989, J.R. Anderson and Milson<sup>1</sup> published the first paper explicitly adopting the ‘rational analysis’ approach to cognition. In the decade since, the approach has been vigorously pursued, whether by name<sup>2–9</sup> or merely in spirit<sup>10–12</sup>. Rational analysis has been the topic of an international conference, involving some of the world’s leading cognitive psychologists and is the focus of the resulting book<sup>13</sup>. But what exactly is rational analysis? How does it relate to other approaches in cognitive science? How does it apply in practice? This review addresses these questions, beginning by distinguishing the style of explanation used in rational analysis from conventional explanation in the cognitive sciences.

## What is rational analysis?

### *Mechanistic and purposive explanation*

A scientific explanation of psychological, biological, or social phenomena can take one of two complementary forms. The first is ‘mechanistic’. Phenomena are explained by analysing their internal causal structure. The second is ‘purposive’. The phenomena are explained in terms of their purpose: what problem they solve.

In biology, purposive explanation concerns the *function* of biological structures and processes (e.g. the function of the heart is to pump blood); and the same style of explanation is applied to animal behaviour (e.g. the function of building nests is to provide a safe shelter for eggs). In social

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