

Table 1 (Johnson et al.). Sources of prespecification

Source of constraint	Examples in brains	Examples in networks
	synapses; specific microcircuitry	weights on connections
Representations	unit cytoarchitecture (neuron types); firing thresholds; transmitter types; heterosynaptic depression; learning rules (e.g., LTP)	activation function; learning algorithm; temperature; momentum; learning rate
Architectures	local number of layers; packing density; recurrence; basic (recurring) cortical circuitry	network type (e.g., recurrent, feedforward); number of layers; number of units in layers
	global connections between brain regions; location of sensory and motor afferents/efferents	expert networks; separate input/output channels
Timing	number of cell divisions during neurogenesis; spatio-temporal waves of synaptic growth and pruning/decay; temporal development of sensory systems	incremental presentation of data; cell division in growing networks; intrinsic changes resulting from node saturation; adaptive learning rates

From Elman et al. 1996.

that more detailed aspects of cortical circuitry are, and that they constrain considerably the types of representations that eventually emerge during development. This, then, is one limitation on plasticity. Another source of constraint, also briefly alluded to by Q&S, is timing. In our book we give a number of examples from real and artificial neural networks in which the relative timing of events critically influences the solutions arrived at. Likewise, Q&S stress need for prolonged gradual exposure and regulated rates of growth of cortical (dendritic) networks.

In addition to these intrinsic constraints on the formation of representations, we suggest that initial biases in the behavior of the infant select particular aspects of the environment for input, thus shaping subsequent brain development. For example, the tendency of newborns to orient to faces biases their input from the environment to that class of stimulus (Johnson & Morton 1991). Thus, we argue for behavioral constructivism in addition to neural constructivism. Of course, these biases in behavior have a neural basis which, we suggest, involves mainly subcortical structures. Specific biases in subcortical structures may provide an additional constraint on the representations that subsequently emerge in cerebral cortex. In short, Q&S's neural constructivism needs to be matched with a mechanism for behavioral constructivism in the infant.

While we are encouraged that our book and Q&S's target article offer a vision of a future constructivist approach to neurocognitive development, there is clearly a long and challenging path ahead. Specifically, there is a need for computational models which incorporate both dynamic and static aspects of brain structure during development, and which speak to the issue of the formation and transformation of hierarchical representations during postnatal cortical development. Only when we have such models is there the possibility of accounting for interesting cognitive changes.

### Cortical development: A progressive and selective mesh, with or without constructivism

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**Abstract:** A credible account of the neurobiology underlying cognitive development cannot afford to ignore the recently demonstrated innate regionalisation of the neocortex as well as the ontogeny of corticocortical

phenomena, only for the latter does the timing of development permit control by external events and this is most likely to occur at later stages in the fine tuning of cortical microcircuitry.

connections. Although progressive processes are implicated in both

Relating mind and brain is laudable. Relating the emergence of mind and brain is positively heroic. Quartz & Sejnowski's (Q&S's) constructivist manifesto attempts just that and takes "environment" as the common denominator. Minds provide representations (of the environment) and environmental factors shape gene expression, which in turn controls development. Hence the philosophers dream: what is to be learnt instructs the means of learning. The notion that environmental factors provide an impetus for progressive as well as selective processes makes for a welcome conceptual change from the excessive reference over the past few years to so called "regressive phenomena" (cell death, axon and synapse elimination). However, a major confusion in the manifesto is made concerning the the environment of minds (which is the object of learning and what we refer to as external events) and the environment of cells (which in a multicellular organism is largely specified by the genome and referred to as the "internal environment"). The constructivist manifesto requires that external events control growth mechanisms. However, much of cortical development occurs in the absence of evoked activity signaling external events, and, although spontaneous activity is frequently reported to play a potentially important role (e.g., McAllister et al. 1996; reviewed in Goodman & Shatz 1993), it is part of the internal environment as defined above.

The development of thalamocortical connectivity shows a progressive acquisition of structure rather than the massive pruning required by selectionist theories; given what we know about the development of ocular dominance columns, Q&S are right to mention it. However, why have they chosen to ignore the literature on the development of connectivity linking cortical areas? First, such connections underlie much of the processing which is *inherently* cortical (synapses driven by the thalamus represent less than 1.6% of total synapses in the cortex; Peters & Payne 1993). Second, unlike in thalamocortical connectivity, where the consensus overwhelmingly favours a limited role of pruning, it has been repeatedly claimed that the adult pattern of corticocortical connections develops via the elimination of widespread connections.

It is surprising that so few studies have examined the development of the functionally defined pathways linking cortical areas. In kittens, several studies did show late elimination of connections between visual cortical areas (e.g., Price & Blakemore 1985). However, progressive phenomena have also been reported. As

Q&S point out, a cardinal feature of representation resides in the topography of connections. A recent quantitative study of the topography of extrinsic and intrinsic cortical connections in cats showed that the divergence values of the bulk of connections in developing pathways were within the adult range, suggesting that this feature of connectivity develops largely independently of selective processes (Kennedy et al. 1994). These studies in the kitten fail to distinguish feedforward and feedback connections. This difficulty can be overcome in the exquisitely compartmentalised extrastriate visual cortex of the primate. Using this model we examined the development of functional feedforward pathways and showed that directed growth plays a major role; the adult pattern of connectivity is accordingly acquired early in development with little or no elimination of inappropriate target axons (Barone et al. 1996).

So far, the development of association feedforward pathways could well be in accord with the constructivist manifesto, although it needs to be stated that even the small amount of developmental pruning observed could reflect important selective processes. However, feedback connections do not show the early specification of the feedforward pathways. Here selection leads to a massive reorganization of the laminar distribution of corticocortical neurons participating in feedback projections (Barone et al. 1995), suggesting that the relative role of progressive and selective mechanisms differs according to the functional role of the cortical pathway (Singer 1995). These findings suggest that understanding the functional role of feedback and feedforward connections gives a better understanding of where one could expect constructivist mechanisms to operate.

The manifesto gives short shrift to the early specification of cortical areas and declares: "the cortex . . . is largely equipotential at early stages" (sect. 4.1.1, para. 2). This is curious because it suggests a selective stance: if the cortex were equipotential, it would have a uniform connectivity so that selective axon loss must be proposed for the emergence of specific regional connections. In any case, the hypothesis of the equipotential cortex is no longer viable in view of recent results with molecular markers showing early regionalization prior to thalamic innervation (Arimatsu et al. 1992; Barbe & Levitt 1991; Cohen-Tannoudji et al. 1994) and axonal tracers showing adult-like distributions of immature corticospinal projections (Meissirel et al. 1993; Oudega et al. 1994). Finally, the concept of an equipotential immature cortex has been definitively refuted by the quantitative analysis of grafting experiments (Ebrahimi-Gaillard & Roger 1996).

The difficult task which remains is to conceptualise the afferent specification by the internal environment (Killackey 1990; O'Leary 1989) with early cortical regionalization (Rakic 1982). Attempts to do this have largely referred to prenatal enucleation experiments in the monkey (Kennedy & Dehay 1993a; Rakic 1988). These experiments show that the dimensions of striate cortex are determined by the number of thalamic afferents and that in their absence, cortex which was destined to acquire striate features instead takes on the phenotypic features of extrastriate cortex, which, however, still continues to display a number of unusual features, possibly of striate origin (Dehay et al. 1996a; 1996b; Rakic et al. 1991). Clearly, the early regionalisation of cortex places important constraints on the amount of instruction that can be derived either from external events or the internal environment.

In conclusion, there are many progressive phenomena in cortical development, particularly in feedforward connections. However, for this to correspond to a constructivist model, external events need to influence the underlying growth processes. The paradigm for such a phenomenon is curiously suggested by numerous reports of cortical plasticity in the adult (reviewed in Kaas 1995), largely unmentioned by the manifesto. That field of research reminds us that the cortex is a universal learning machine and raises renewed interest in the continuity hypothesis (Pinker 1984). It links adult and developmental plasticity (Cramer & Sur 1995) and suggests a neotenuous phenomenon as a central feature

of cortical function. More specifically, the manifesto needs to pay particular attention to the timing of cortical development and to recognise the improbability of external events influencing early development (Kennedy & Dehay 1993b). Because much of cortical pathway formation occurs prior to activity evoked by the external world reaching the cortex, it seems likely that constructivist control concerns the late fine tuning of the feedback cortical connections required for cortical function.

## From neural constructivism to children's cognitive development: Bridging the gap

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**Abstract:** Missing from Quartz & Sejnowski's (Q&S's) unique and valuable effort to relate cognitive development to neural constructivism is an examination of the global emergent properties of adding new neural circuits. Such emergent properties can be studied with computational models. Modeling with generative connectionist networks shows that synaptogenic mechanisms can account for progressive increases in children's representational power.

Quartz & Sejnowski describe an exciting new approach to relating brain development and cognitive development. Although constructivist accounts of cognitive development have a long history (e.g., Case 1985; Fischer 1980; Piaget 1970), there have been few attempts to ground the principles of constructivist development in a neural or biological substrate. The few attempts have either failed to relate development to specific brain processes or have failed to show how neural changes increase representational power. For example, Piaget (1980) describes cognitive development in terms of biologically plausible competitive mechanisms but fails to specify how these mechanisms are implemented in the brain. In contrast, others – such as Case (1992), who attributes much of cognitive development to greater myelination in the frontal lobes, or Fischer (1994), who argues that patterns of cyclical brain activity correspond to stage like transitions in brain reorganization – fail to specify how these neural processes increase representational power. Q&S are to be commended for tackling both sides of the issue.

However, an important element is missing from Q&S's argument if they wish to support the hypothesis that the neural mechanisms they describe actually underlie the development of behaviors observed in children. They suggest a means by which constructivist development can occur at the neural level but it is possible that other, more global processes dominate children's cognitive development. Indeed, the global interactions that emerge from a complex system may overshadow the effects of constructivist development at the level of individual neurons. To substantiate the claim that a constructivist neural mechanism empowers a system to learn complex relationships in the same way children do, it is necessary to explore whether the developmental profiles of a generative neural network match the developmental profiles observed in real children when presented with identical learning tasks.

One way to test this is through computer modeling. Computer models of child development provide a way to investigate the mechanisms that may underlie observed behaviors (Halford & Simon 1995). A mechanism that does not produce the correct developmental profile can be ruled out as a candidate. Generative connectionist networks (networks that grow their own architectures as part of learning) are being explored as models of constructivist cognitive development (Mareschal & Shultz 1996). Models