area of the postsynaptic membrane where there is a high density of receptors) in the intermediate and medial hypertensum ventricle (IMHV), a region that is crucially involved in learning during imprinting (Horn 1985). There were no significant learning-related changes in the number of presynaptic boutons or dendritic spines. The increase in PSD was limited to spine synapses: there was no such increase in synapses directly on the shaft of dendrites. Furthermore, the increase only occurred in synapses in the left IMHV, not in the right, which is consistent with other evidence that assigns a long-term storage function to the left IMHV (Horn 1985). Similarly, McCabe and Horn (1986) reported a significant positive correlation between the number of NMDA receptors and the strength of imprinting in the left IMHV only.

Using the Golgi method of staining, some authors have reported changes in the number of dendritic spines in some brain areas after early learning. Patel et al. (1988) reported, *inter alia*, a small, nonsignificant increase in the number of dendritic spines per unit length of dendrite in the left IMHV of chicks that had learned a passive avoidance task, compared to chicks that had not. In contrast, Wallhäusser and Scheich (1987) reported a reduction in the number of spines in the left IMHV of chicks that had learned an auditory imprinting session: guinea fowl chicks. The changes were found in a forebrain region (MNH) that may have some overlap with the anterior part of the IMHV. Interestingly, a recent combined Golgi and electron-microscopic analysis suggests that although after auditory imprinting there is a reduction in the number of synapses in the MNH, the number of the PSDs of the remaining synapses increases (Scheich 1990).

Unlike QES (sect. 3), Nottebohm (1991) and co-workers have suggested that the entire neuron is the brain's basic computational unit, when they reported neurogenesis in the brain of canaries and zebra finches (which occurs for some time after hatching and into adulthood). It is not clear whether these new neurons, which became functionally integrated into existing circuits, are necessary for the central representation of song. For instance, there is no relationship between neurogenesis and song quality or whether or not the birds modify their songs in adulthood. Also, neurogenesis occurs at the forebrain and not just in song-related regions.

Taken together, the avian data do not support a role for the neuron as a computational unit. However, even if we assume that “clustering” and “volume learning” (sect. 3) are important features in the developing brain, the synapse is still the ultimate unit of neural plasticity, and the avian data to which I have referred suggest that the neuronal substrates of learning and memory are crucially involved in the neural representation of information. Although changes in the number of synapses in the spine may play a role, it would seem that increases but probably also decreases in PSDs and concurrent receptor numbers are the changes that matter. Thus, changes in the strength of existing connections are important. In line with theoretical considerations that have been formally incorporated in a model of early learning (Bateson & Horn 1994). As QES states, for learning to occur “there must be some built-in assumptions” (sect. 4.3.1). The architecture of the Bateson and Horn model also allows for the influence of predispositions, in line with the behavioral and neurological data on the development of filial preferences in the chick (Bolhuis 1994; Horn 1985).

The target article acknowledges the existence of regressive events during learning and development, and their theoretical importance (e.g., sects. 2.1.1, 2.2.1, 2.3.2). How can constructive and regressive findings be reconciled in an "interactionist" theory? Greenough et al. (1997) advanced such a theory by associating synaptic selection and synapse formation, respectively, with "experience-dependent" and "experience-dependent" information storage. This distinction is a functional one, based on the type of information stored, information which is ubiquitous and identical for all members of the species in the former, and unique to the individual in the latter. I have argued (sect. 4.3.1) that using these terms at two different levels of explanation limits their usefulness: moreover, the evidence from the avian work does not support the distinction. In reality, both "experience-dependent" and "experience-expectant" information may be stored during learning and development and is not impossible to tease apart the mechanisms involved in these two putative processes, let alone relate them to specific neural changes.

In defense of learning by selection: Neurobiological and behavioral evidence revisited

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Abstract: Quarts & Sejnowski's (QES) constructivist manifesto promotes a return to an extreme form of empiricism. In defense of learning by selection, we argue that not the neurobiological level all the data presented by QES in support of their constructivist model are in fact compatible with a model comprising multiple overlapping stages of synaptic overproduction and selection. We briefly review developmental studies at the behavioral level in birds providing evidence in favor of a selectivist view of development.

Our understanding of cognitive functions such as language and calculation is likely to make considerable progress once we begin to uncover not merely the algorithms that underlie their acquisition in the child's mind, but also their biological basis in the child's brain (Changeux & Dehaene 1989; Dehaene & Changeux 1985; Diamond 1988). What, however, is the appropriate theoretical framework in which developmental cognitive neuroscience research should be framed? Quarts & Sejnowski's "constructivist manifesto," although purportedly rejecting the classic dichotomy between empiricism and nativism, actually promotes a return to an extreme form of empiricism, in which a "largely equipotential cortex" (sect. 4.3.1) becomes specialized through "directed growth" (sect. 2.2.1) under the specification of environmental inputs. We strongly disagree with this point of view and would like to present here a brief defense of the selectivist framework of cognitive and neural development (Changeux & Dehaene 1999, Edelman 1997).

*Multiple waves of synaptic overproduction and selection.* Most of the arguments that QES present against learning by selection arise from a microstructural selectivism of cognitive and neural development. In section 2, QES describe a simplistic version of selectivism that "divides development into two discrete stages": first, the intrinsic production of "prerepresentations," and second, their selective elimination or stabilization. QES then reach the far-fetched conclusion that "for selectivism, development marks a reduction in representational complexity" (a definition that seems to better capture the manifestations of aging). This oversimplified characterization is then easily dismissed as being incompatible with numerous data that underscore the progressive enrichment in synaptic numbers, axonal arborizations, and dendritic trees that accompany cognitive development.

Selectivist theories of learning (e.g., Changeux 1985; Changeux & Dehaene 1989; and Edelman 1987) are considerably more subtle than suggested by QES's summary. Most important, they allow for multiple, overlapping waves of synaptic development followed by selection, thus providing a basis for understanding the increase in nervous system complexity during development. Here, for instance, is how Changeux (1985, pp. 248-49) describes this process:

The 10,000 or so synapses per cortical neurons are not established immediately. On the contrary, they proliferate in successive waves from birth to puberty in man. With each wave, there is transient redundancy and selective stabilization. This causes a series of critical periods when activity exerts a regulatory effect... One has the impression that the system becomes more and more ordered as it receives...
Commentary/Quartz & Sejnowski: Cognitive development processing. Although Piaget viewed numerical development as a slow, protracted process, we now know that size- and location-invariant discrimination of number is within the grasp of 3-month-old infants (Starkey & Cooper 1980; Treher & Wilcox 1984) and even of newborns (Ansell & Reating 1985; Bilijec-Bahri et al. 1991). Four-and-one-half-month-olds exhibit elementary set addition and subtraction abilities (Kochlin et al., submitted; Vynne 1992), and 6-month-olds show evidence of cross-modal matching of auditory and visual numerosity (Starkey et al. 1985; 1989; see also Moore et al. 1987). Such data seem difficult to explain by constructive learning, for it is hard to see what kind of environmental input available to young infants could teach them object addition or cross-modal numerical correspondence (two objects do not necessarily make two sounds, nor do two sounds necessarily come from two objects). Much of early numerical development, however, can be accounted for by a model in which an innately specified array of numerosity detectors serves as the basis for subsequent learning by selection (Dehaene & Changeux 1992).

Language acquisition during the first year of life also provides a rich set of data that mitigates against constructive learning, most likely with multiple critical periods. From birth, human infants discriminate phonemic contrasts (Bertoncini et al. 1987; Eimas et al. 1971), including those that are not used in their maternal language (Trehub 1983). This capacity has been shown to be present in early left-hemispheric specialization for linguistic stimuli (Bertoncini et al. 1989; Dehaene-Lambertz & Dehaene 1994), thus contrasting Q&S’s notion of a “largely equipotential cortex.” Most important, the first year of life shows a decrease in phoneme discrimination abilities. At 8 to 10 months of age, infants still discriminate non-native phonemic contrasts, but by 10 to 12 months they lose this ability and maintain only native phonemic categories (Weker & Lakone 1986). This provides direct evidence for a selective, environment-dependent loss of initial abilities, as predicted by selectionist theory. A similar phenomenon occurs for vowels at an even earlier age (six months, Kuhl et al. 1992). It is now suggested that discrimination of language sounds follows a similar developmental pattern (Meier & Christoph 1995). Newborns discriminate sentences drawn from two different languages (Meier et al. 1985), including languages that they have never heard (Nuzzi et al., in press), whereas two-month-olds are only able to discriminate their maternal language from another language, but not two foreign languages from one another (Meier et al. 1992), again suggesting a selective loss of speech perception abilities in the course of acquiring a specific language. To be sure, learning plays a major role in language development during the first year of life – but it is a form of learning that capitalizes on an initial repertoire of dedicated processes that are already functional right from birth.

Neurotrophic factors, neuronal selectionism, and neuronal proliferation

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Abstract. Quartz & Sejnowski’s (Q&S) disregard evidence that suggests that their view of selection is inadequate and they ignore recent results concerning the role of neurotrophic factors in synaptic remodelling. They misrepresent neuronal selectionism and thus erect a straw-man argument. Finally, the results discussed in section 4.1 require neuronal proliferation, but this does not occur during the period of neuronal development of relevance here.

Selectionist accounts are, for the most part, inadequate theories of neuronal development; much evidence suggests that constructive events occur at least as importantly as regulatory events (e.g., Purves 1994). For this reason, we are developing models of the formation

Figure 1 (Dehaene-Lambertz & Dehaene). Contrary to Quartz & Sejnowski’s suggestions, learning by selection, when proceeding in multiple stages, is not incompatible with neurodevelopmental evidence. (a) Multiple waves of synaptic overproduction followed by synaptic density remains stable over long period of time, as shown in Fig. 4(a) of Q&S’s article (Huttenlocher 1979). (b) Multiple, possibly overlapping phases of blind axonal sprouting followed by selection result in increasingly refined targeting of connections, thus giving the impression of directed growth.