area of the postsynaptic membrane where there is a high density of receptors) in the intermediate and medial hyperstriatum ventrale (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 shafts 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 (1988) 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 dendritic spines on a particular class of neurones, after an auditory imprinting session in 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 spines in the MNH, the size of the PSDs of the remaining synapses increases (Scheich 1996).

Unlike Q&S (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 zebrafinches (which occurs for some time after hatching and into adulthood). It is not clear whether these new neurons, which become functionally integrated into existing circuits, are necessary for the central representation of song. For instance, there is no relationship between neurogenesis and seasonality or whether or not the birds modify their songs in adulthood. Also, neurogenesis occurs across 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 changes in synaptic strength are crucially involved in neural representation of information. Although changes in the number of synaptic spines 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 Q&S state, 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 behavioural and neurobiological data on the development of filial prefences 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. (1987) advanced such a theory in associating synapse selection and synapse formation, respectively, with "experience-expectant" 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 (Bolhuis 1994) 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. It seems 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

G. Dehaene-Lambertz[a] and Stanislas Dehaene[b]

[a]*Laboratoire de Sciences Cognitives et Psycholinguistique, 75270 Paris cedex 06, France.* **ghis@lscp.ehess.fr;** [b]*INSERM U334, CHFJ CEA, 91401 Orsay, France.* **stan@lscp.ehess.fr**

Abstract: Quartz & Sejnowski's (Q&S's) constructivist manifesto promotes a return to an extreme form of empiricism. In defense of learning by selection, we argue that at the neurobiological level all the data presented by Q&S in support of their constructive 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 humans providing evidence in favor of a selectionist 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 1993; Diamond 1988). What, however, is the appropriate theoretical framework in which developmental cognitive neuroscience research should be framed? Quartz & 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 selectionist framework of cognitive and neural development (Changeux & Dehaene 1989; Edelman 1987).

Multiple waves of synaptic overproduction and selection. Most of the arguments that Q&S present against learning by selection arise from a misconstrual of selectionist theories of cognitive and neural development. In section 2, Q&S describe a simplistic version of selectionism that "divides development into two discrete stages": first, the intrinsic production of "prerepresentations," and second, their selective elimination or stabilization. Q&S then reach the far-fetched conclusion that "for selectionism, 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.

Selectionist theories of learning, (e.g., Changeux 1985; Changeux & Dehaene 1989; and Edelman 1987) are considerably more subtle than suggested by Q&S'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 neuron 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 exercises a regulatory effect . . . One has the impression that the system becomes more and more ordered as it receives «instructions»

...out the environment. If the theory proposed here is correct, spontaneous or evoked activity is effective only if neurons and their connections already exist before interaction with the outside world takes place. Epigenetic selection acts on preformed synaptic substrates. To learn is to stabilize preestablished synaptic combinations, and to eliminate the surplus.

Once it is recognized that synaptic overproduction and selection can occur simultaneously and in multiple waves, rather than in a discrete two-step process, all the neurobiological phenomena that Q&S claim refute selectionism and support constructivism actually become explainable within a selectionist framework (see Fig. 1). In this framework, the progressive increase in axonal complexity, for instance, is viewed as resulting from a blind process of overproduction of axonal branches, while their increasing targeting to specific layers is taken to reflect the elimination of misplaced or nonfunctional branches.

In addition to explaining the major phenomena of neural growth, selectionism also releases axons and dendrites from a considerable computational load. According to Q&S's constructivism, the nervous system is subject to "directed growth" and dendrites act "as though they are looking for afferent inputs" (sect. 2.3.3). They even "redirect their growth to find active afferents" (sect. 2.3.3) and they "actively seek out incoming activity" (sect. 2.3.4). We think that the use of this mentalistic vocabulary, which treats single dendrites as cognitive agents, makes for a misleading and ill-specified analogy, which in selectionist theories is replaced by a simple, explicit, and empirically testable mechanism for stabilization (see Fig. 1). Like the nervous system, the immune system also seems to react "intelligently" to external inputs – but the mechanism underlying this seemingly directed response is selectionist in nature. Whether neural development will also be accounted for by selectionist mechanisms remains an open issue at present, but our point is that selectionism remains a viable theory in the face of current neurobiological data (for a recent in depth discussion, see Katz & Shatz 1996).

Cognitive developmental evidence for learning by selection. At the cognitive level, the Piagetian notion that mental representations are constructed through a progressive instruction by environmental inputs is now obsolete. Ample evidence indicates that human infants exhibit, very early on, a degree of competence in specific domains of cognitive functioning that seems hard to explain by "constructive learning." One such domain is number

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 2-month-old infants (Starkey & Cooper 1980; Treiber & Wilcox 1984) and even of newborns (Antell & Keating 1983; Bijeljac-Babic et al. 1991). Four-and-one-half-month-olds exhibit elementary set addition and substraction abilities (Koechlin et al., submitted; Wynn 1992), and 6-month-olds show evidence of cross-modal matching of auditory and visual numerosity (Starkey et al. 1983; 1990; 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 1993).

Language acquisition during the first year of life also provides a rich set of data that militates against constructive learning and supports a selectionist view of development, 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 1976). This capacity has been shown to depend on an early left-hemispheric lateralization for linguistic stimuli (Bertoncini et al. 1989; Dehaene-Lambertz & Dehaene 1994), thus contradicting 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 (Werker & Lalonde 1988). 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 prosody follows a similar developmental pattern (Mehler & Christophe 1995). Newborns discriminate sentences drawn from two different languages (Mehler et al. 1988), including languages that they have never heard (Nazzi 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 (Mehler et al. 1988), 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.
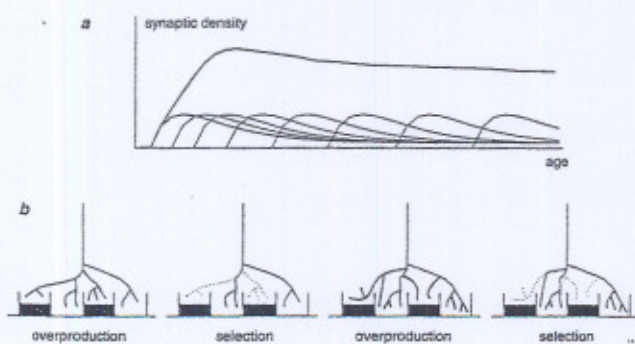

Figure 1 (Dehaene-Lambertz & Dehaene).   Contrary to Quartz & Sejnowski's suggestions, learning by selection, when proceeding in multiple stages, is not incompatible with neurodevelopmental evidence. (*a*) Multiple waves of synaptic overproduction followed by selective elimination (bottom curves) add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

Neurotrophic factors, neuronal selectionism, and neuronal proliferation

T. Elliott[1] and N. R. Shadbolt
Department of Psychology, University of Nottingham, Nottingham, NG7 2RD, United Kingdom. te@proteus.psyc.nott.ac.uk; nrs@psyc.nott.ac.uk

Abstract: Quartz & Sejnowski (Q&S) disregard evidence that suggests that their view of dendrites 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 4.2 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 are at least as important as regressive events (e.g., Purves 1994). For this reason, we are developing models of the formation