Commentary on Quartz and Sejnowski, "The neural basis of cognitive development: A constructivist manifesto" *Behavioral and Brain Sciences* 20: 564-565.

So many problems, so little time: Evolution and the dendrite

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Abstract: The multiple levels of analysis that Quartz & Sejnowski (Q&S) bring to bear on the phenomenon of activity-driven dendritic growth show the tight linkage of explanations from the cellular to the cognitive level. To show how multiple control regimes can intersect at the same site, I further elaborate an example of a developmental problem solved at the axodendritic connection: that of population matching.

Developmental biology, as invented by evolution, acts as if determined to confound standard hypothesis-testing methods. When asked whether Mechanism A or B is used to implement a particular developmental task (for tasks ranging from the production of trophic factors, to the organization of topographic maps, to establishment of the circuitry for syntax in language), the answer increasingly appears to be A and B (and C, and D, etc.). Conversely, if a phenomenon asks for explanation, such as developmental cell death, or in Q&S's case, activity-driven dendritic growth, it is becoming commonplace that what appears to be a single mechanism subserves a number of different functions and exists at a number of organizational levels.

Things become more difficult still when natural selection, having little interest in the form of intellectual bookkeeping we call "levels of analysis," not only multiplies mechanisms but mixes their levels. The formal separability of levels of analysis has been much discussed (Fodor 1992). In the particular case where an organizing force such as evolution acts across "levels," philosophic separation of levels has produced an *apparent* intellectual clarity that has in fact hopelessly muddled understanding of the actual state of affairs. Sejnowski and colleagues are to be highly congratulated for this article, as well as others, which show another of the many ways perception, cognition, development, and physical mechanism overlay: Gold's theorem and rules for dendritic growth do belong in the same article! In this commentary, I would like to point out another multiple-level, multiple-mechanism conjunction in the case of developing dendrites.

In addition to the unusual challenge of representing the informational structure of the outside world, neurons are posed with some physical challenges in early development. They must send axons to vicinities where they have some chance of encountering their proper targets, determine whether that has occurred, and roughly calibrate the numbers of neurons in connecting populations, which depends upon a reciprocal supply of trophic factors as one of several mechanisms. Q&S have discussed the problem of pathway selection and reduction of developmental "errors" in their target article; I would like to discuss briefly the problem of population matching, as it shows some differences in the behavior of axons and dendrites from those highlighted by Q&S. There are several games in progress on the dendritic playing field.

Convergence, the fan-in of presynaptic cells to postsynaptic cells, varies widely in the nervous system. In some cases, for example, the ratio of projecting thalamic axons to isocortical neurons, convergence seems virtually unconstrained and a potential source of plasticity (Finlay & Darlington 1995); in others, as in regions of the retina (Rowe 1991) and in some aspects of cerebellar circuity (Williams & Herrup 1988), convergence seems highly constrained and of immediate functional consequence. The developmental regulation of convergence ratios from retina to tectum in developing mammals (Xiong et al. 1994; reviewed in Xiong & Finlay 1996) and during regeneration (Hayes & Meyer 1988) shows that the action is in the axon. The visual receptive field size of a normal tectal neuron does not show wide variability in the adult, and this receptive field size is defended against a wide range of experimentally induced variations in the total number of retinal neurons compared to tectal neurons (Pallas & Finlay 1989). During development, this problem must be solved in the perplex-

ing context of early overabundance of neurons. In this case, the numbers of both retinal and tectal neurons are several times in excess of their mature numbers. What matches what? Essentially, tectal neurons proceed to their adult number of neurons through apoptosis and to their adult state of synaptic density uninfluenced by excessive numbers of axons in the input retinal population. Retinal neurons buffer their own rate of survival through their axons: fan-out is sacrificed to fan-in, so that axonal arbors are much reduced in size (up to tenfold) when convergence ratios are high. The number of contacts from any one retinal neuron to a tectal neuron is about the same, but many fewer tectal neurons are contacted by each retinal axon. Conserved target dendritic volume sets the upper and lower limit on retinal neuron number, with plasticity within this range permitted by axonal variability. It is of interest in light of Q&S's article that a functional reset of the size of a system, as might happen in the case of neural structures influenced by gonadal steroids (Sengelaub 1989) or by unusual learning regimes (Turner & Greenough 1985), can and does happen through dendritic structure. More time could be spent on the specific empirical question about the active role of the axon, somewhat neglected in Q&S's discussion, but that is a separate issue.

Overall, Q&S's multilevel style of analysis is to be much applauded, and the example set out here adds an additional regulatory problem for the axo-dendritic interface. At least three problems involve the axo-dendritic interface in early development: target selection; population matching, and the activity-dependent dendritic structuring that was the main focus of Q&S. Each problem uses the information of the correlated firing of the input array, but each under a different control regime. We might construe some problems as more biological in level (e.g., acquiring adequate trophic support), others as more "cognitive" (e.g., representing the correlational structure of the input), but, in all cases, it's the same dendrite solving the problem.