Selectionist mechanisms: A framework for interactionism

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The nature/nurture dichotomy has been commonly used as a paradigm for the experimental study of the complex interactions between an organism and its environment. That it turned out to be an oversimplification is no surprise, but it does not entail returning to such extreme interactionism as Johnston suggests. The contention that there is "a host of potential contributors to the development of the organism" can hardly be denied. Being neutral with respect to the nature of the interaction between these contributors, interactionism appears too powerful to suffer refutation by experiment.

Selectionist (or Darwinist) theories of learning (Changeux et al. 1984; Changeux & Dehaene, in press; Edelman 1978; 1987; see also Jerne 1967) offer a third way between the oversimplification of the nature/nurture approach and the excessive generality of interactionism. Selectionist theories belong to the interactionist framework since they attribute adult behavior to an interaction of genetic potentials and environmental pressures. However, the rules of this interaction are clearly defined. In their full generality, selectionist theories apply to any two successive levels of study of a biological system (Changeux & Dehaene, in press). It assumed that lower levels function as generators of a diversity of transient forms, produced by a combinatorial rule, which are later selectively stabilized or eliminated at a higher level according to their fitness (or resonance) with environmental or internal cues. For example, in the development of the neuromuscular junction in vertebrates, multiple innervation governed by molecular mechanisms of "blind" growth precedes a pruning of functional nerve endings by neuronal activity, which ultimately leaves one axon terminal per muscle fiber.

Another example at a higher level is the initially wide "genetic envelope" (Changeux & Danchin 1976) that human neonates possess for discriminating linguistic sounds (Eimas 1975), which gets reduced as the baby loses the capacity to discriminate sounds that do not belong to his maternal language (Werker & Tees 1984). These examples do not imply that selection is always a two-stage process: In general, there may be several hierarchically organized phases of diversification followed by selective stabilization, each taking place within the structures laid down by the preceding one (see Nottebohm, 1981, for a suggestion that seasonal dendritic growth underlies periodic relearning in the canary). [See also Ebbesson: "Evolution and Ontogeny of Neural Circuits" *BBS* 7(3) 1984.]

Applying selectionist theories to birdsong acquisition, although not mentioned by Johnston, is not recent (see Marler & Peters 1982b). Plastic song initially contains a wide diversity of syllables, most of which will not be retained in adult song. The well-documented process of syllabic attrition (Marler & Peters 1982b) has been interpreted as a selection by matching of early productions with syllables memorized in the first weeks of life (Marler & Peters 1981). The selectivity of learning to conspecific material observed in birds like *Melospiza georgiana* (Marler & Peters 1977) may result from constraints in the initial "genetic envelope": The set of "pre-representations" produced at the early stages of song development should not in general provide the potential to learn any song.

We have recently proposed a formal neuronal model of birdsong acquisition (Dehaene et al. 1987). The model applies to song memorization (sensory learning), which is supposed to be as selective as the later sensory-motor or imitation phase. Three biologically plausible properties are simulated: (1) "synaptic triads," which model the possibility that the efficacy of a synapse is modulated by a neighboring synapse of the same postsynaptic neuron via allosteric modifications of receptor conformations, (2) self-excitatory clusters of neurons which can maintain a sustained activity and are organized into superimposed layers termed sensory, input, and internal, and (3) a Hebbian modification rule which stabilizes connections when their presynaptic activation matches the postsynaptic activity of their target cell. In the simulated network, some clusters act as sequence detectors of the input song. These detectors respond initially to diverse transitions and progressively acquire more selectivity to the particular song which is learned. The initial connectivity provides the network with the capacity of internally producing a diversity of songs. The learning rule progressively prunes this repertoire according to its resonance with the song heard.

Our model, and selectionist theories of birdsong acquisition in general, suggest a number of experimental tests that are not considered by Johnston. Johnston is basically right in proposing to stop the isolation rearing paradigm. But rather than studying more closely the social aspects and functional outcomes of birdsong, which is likely to add more complexity but little understanding to the acquisition process, we propose to explore further the learning mechanism itself. Very little is known about how song is memorized in the first weeks of life. Our model proposes that the sensory phase is governed by the same principles of selection as the later imitation phase. Initial responding to a global repertoire, followed by subsequent narrowing and tuning of sensory capacities is predicted. At the neural level, single-cell recordings in the HVc nucleus of the white-crowned sparrow (Konishi 1985; Margoliash 1983) have led to the identification of sequence-specific neurons. Similar recordings at different ages in the course of learning should reveal a progressive tuning of sequence-detecting neurons to more and more restricted portions of the song. At the behavioral level, it should be possible to selectively maintain song elements that are normally eliminated by exposing the bird early to synthetic songs containing those elements. Supporting this prediction, Kreutzer (1987) describes a population of cirl bundings (*Emberiza cirlus*) whose repertoire contains an atypical, normally eliminated song which resembles the productions of isolation-reared birds.

To conclude, selectionist theories of learning adhere to the interactionist view that adult behavior results from an interaction between internal potential and external constraints, but with definite limits on this interaction. The notion of "learning by instinct" (Gould & Marler 1987) emphasizes a similar idea. Recently, we have suggested (Changeux & Dehaene, in press) that similar selectionist mechanisms may extend to the higher level of human reasoning. At short time scales, "mental models" and rules of behavior would be selected according to their congruence with the current goal of the organism. The prefrontal cortex would generate a diversity of "models" and rules available for later selection. If such a theory of "mental Darwinism" is correct, and if selection is indeed the key to brain function, song learning in birds might be a useful animal model for the study of its neural bases.

Nature/nurture and other dichotomies

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Johnston's target article is a clear and valuable exposition of the so-called interactionist position that is descended intellectually from the work of Anastasi (1958), Carmichael (1925), Kuo (1967), Lehrman (1953), and Schneirla (1957). Among its main points are the emphasis on the impact of nonspecific experience upon