



HYPOTHESIS

Epigenetics and the evolution of instincts

Instincts may evolve from learning and share the same cellular and molecular mechanisms

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An animal mind is not born as an empty canvas: Bottlenose dolphins know how to swim and honey bees know how to dance without ever having learned these skills. Little is known about how animals acquire the instincts that enable such innate behavior. Instincts are widely held to be ancestral to learned behavior. Some have been elegantly analyzed at the cellular and molecular levels, but general principles do not exist. Based on recent research, we argue instead that instincts evolve from learning and are therefore served by the same general principles that explain learning.

Consider individuals in an ancestral population that use behavioral plasticity to respond adaptively to their environment (1, 2).

If this adaptive response increases fitness, then natural selection should favor animals that manifest the trait earlier in development or with less practice (3). Selection acting to adjust the timing and extent of plasticity can thus produce an instinct. The selective forces would depend on the environment. In certain environments, behavioral plasticity might be favored, but in other environments, more stereotyped behavior might prove superior (1, 3). This process need not result in the programming of every single detail of an instinct; all that is needed is an initial behavioral bias followed by a process of experience-dependent refinement (4), driven by predictable patterns of environmental reinforcement.

This hypothesis is consistent with the “plasticity first” model of evolution, which states that plasticity can precede and facilitate evolutionary adaptation (1). The plausibility of this model has increased dramatically with the advent of behavioral genomics. We now know that the genome responds dynamically to a range of behaviorally relevant stimuli, often with massive changes in brain gene expression (2). Plasticity-first models have been

used to explain various phenomena, including the evolution of personality differences in stickleback fish, behavioral diversification in Darwin’s finches, and rapid anatomical and behavioral evolution in primates (2, 5).

Also, it is possible that some instincts evolved via the more traditional “mutation first” model of evolution. In this case, mutations cause changes in the timing of the development of neural circuitry, for example, from postnatal to prenatal. In either case, once evolved, the effectiveness of innate components of a behavior can be enhanced by the evolution of more complex forms of learning as these components become increasingly refined by natural selection. Learned and instinctive components of behavior are intertwined and should therefore be regulated by the same general neural mechanisms.

Evidence from neuroscience supports the idea of a unified model of behavior. For example, recent results from bees and flies show that both innate and learned olfactory responses are governed by the same neural circuits (6). Similarly, in rodents, the neural circuits organizing innate and learned fear

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Honey bees instinctively know how to use movements and sounds to communicate to their hive mates about the location and quality of flower patches in the environment.

responses overlap, and serotonin modulation in the amygdala determines which response is strongest (7).

Tierney first proposed in 1986 (4) that instincts can evolve from behavioral plasticity, but the hypothesis was not widely accepted, perhaps because there was no known mechanism. Now there is a mechanism, namely epigenetics. DNA methylation, histone modifications, and noncoding RNAs all exert profound effects on gene expression without changing DNA sequence. These mechanisms are critical for orchestrating nervous system development and enabling learning-related neural plasticity (8).

For example, when a mouse has experienced fear of something, changes in DNA methylation and chromatin structure in neurons of the hippocampus help stabilize long-term changes in neural circuits. These changes help the mouse to remember what has been learned and support the establishment of new behavioral responses (8). Epigenetic mechanisms that support instinct by operating on developmental time scales also support learning by operating on physiological time scales. Evolutionary changes in epigenetic mechanisms may sculpt a learned behavior into an instinct by decreasing its dependence on external stimuli in favor of an internally regulated program of neural development (see the figure).

There is evidence for such epigenetically driven evolutionary changes in behavior. For example, differences in innate aggression levels between races of honey bees can be attributed to evolutionary changes in brain gene expression that also control the onset of aggressive behavior when threatened (2). These kinds of changes can also explain more contemporary developments, including new innate aspects of mating and foraging behavior in house finches associated with their North American invasion 75 years ago, and new innate changes in the frequency and structure of song communication in populations of several bird species now living in urban environments (1). We propose that these new instincts have emerged through evolutionary genetic changes that acted on initially plastic behavioral responses (2, 3).

There is evidence for experience-dependent transgenerational changes in behavior. Female rats that exhibit lower reactivity to stress lick, groom, and nurse their pups extensively. Their offspring also react less to stress. These behavioral changes are associated with epigenetic changes in the hippocampus (methylation of genes involved with

hormone signaling and changes in the chromatin structure around neuronal growth factor genes). Pharmacological manipulations show a causal relationship between methylation and chromatin remodeling in the hippocampus and low stress reactivity (8, 9). Thus, the behavior of low stress-reactive mothers toward their pups causes epigenetic changes in the pup brains for lowered stress response (8, 9).

More provocatively, mice trained to fear a specific odor can transmit this bias to their offspring, apparently via changes in methylation in the germ line that affect the expression of the relevant olfactory receptor genes (10). The offspring of these mice were both more sensitive to the fear-conditioned odor and learned to fear it more rapidly than their parents. Whether environmentally triggered epigenetic changes can persist through the germ line in mammals to influence the next generation remains controversial (11). If epigenetics can mediate a transgenerational inheritance of behavioral biases (either be-

haviorally mediated or by direct molecular actions), this would provide a mechanism for the rapid transformation of learned behavior to an instinct. However, our hypothesis does not depend on such direct effects.

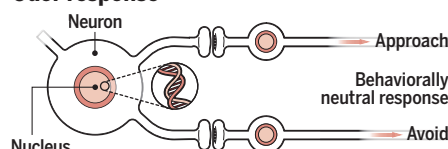
A unified model of behavior—one that employs the same cellular and molecular mechanisms to explain both instinct and learning—will lead to new lines of investigation. Consider the question of the formation of an instinct in light of what we know about the formation of a memory. Learning involves experience-dependent strengthening of specific synapses. If learning is defined by the notion that neurons that “fire together, wire together” (12), how do instincts get wired during development in the absence of experience-dependent neuronal firing? In the case of human speech and hearing, neural development is shaped by experience in utero (13). Could epigenetic mechanisms that regulate changes in gene expression related to long-term memories play similar roles during development to form instincts?

Turning the tables, we also expect that instincts can teach us about learning. Despite excellent progress in localizing networks of neurons that encode specific memories (14), understanding of the physical embodiment of memories is limited. Perhaps instincts can provide the necessary clues. Some instincts, like monogamy in prairie voles, song communication in zebra finches, and sun-compass navigation in monarch butterflies (15), have been traced to specific neuroanatomical features or networks. Considering an instinct as an “ancestral memory” of a specific response to the environment may help to guide efforts to understand the physical basis of memory. ■

How an instinct may evolve from a learned response

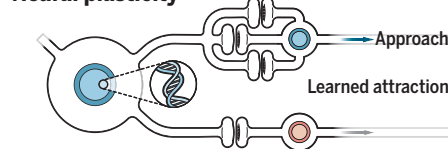
Attraction to a particular odor can develop by epigenetic systems stabilizing structural changes in a neural circuit. These changes could initially result from learning-dependent plasticity, or the circuit could be established during development. Evolutionary processes can adjust the extent to which behavioral response is learned or instinctive by acting on where, when, and how epigenetic mechanisms operate.

Odor response



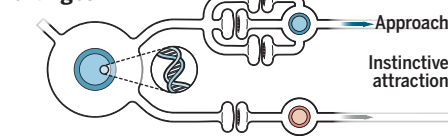
Over physiological time, epigenetic changes stabilize functional changes in neural circuits to establish new behavioral responses.

Neural plasticity



Over evolutionary time, the action of natural selection on epigenetic systems results in the same functional changes, but in the absence of learning.

Developmental changes



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