Plasticity

Important work emerging from developmental biology over the past two decades emphasizes the ubiquity and importance of phenotypic plasticity (Pigliucci 2001, 2005; Pigliucci, Murren, and Schlichting 2006; West-Eberhard 2003). The term is used broadly to talk about genotypes that can produce markedly different phenotypes in different environments. The metaphor of "plasticity" suggests malleability or direct impression, and these metaphors correspond well to what biologists call "passive plasticity." But many important instances—those that biologists describe as "active plasticity"—fit the metaphor of response much better. Whereas passive plasticity is a matter of mere vulnerability to environmental stresses and results in unregulated change in the organism, active plasticity is expressed in complex and coordinated change, often integrating adjustments in morphology, physiology, behavior, and even life history, regulated by means of complex multilevel feedback processes (Whitman and Agrawal 2009). Two birds with the same genotype might differ in color because one has lacked access to the nutrients that are needed to produce a certain pigment in its plumage—an instance of passive plasticity. Or they might differ because one has put on breeding plumage and the other has not, owing to their exposure to differing local seasonal cues—an instance of active plasticity. In the latter case—but not the former—the change in plumage color is just one part of a suite of coordinated changes. A male bird putting on breeding plumage will also adjust his social behavior (courting potential mates and threatening potential rivals, for example) and may build a nest or bower or begin signaling or patrolling to defend his territory. He will almost certainly change his song patterns and may develop brightly colored patches of exposed skin on his face or legs or even grow special plates that change the apparent shape and color of his bill. These visible changes—and the underlying physiological changes that make them possible, providing additional neurotransmitters, pigments, blood flow, and nutrients—are all controlled by hormone levels that themselves change in response to environmental triggers.

Developmental biologists also distinguish between adaptive and nonadaptive plasticity, where adaptive plasticity results from the operation of an evolved mechanism that allows the organism to tap different developmental or behavioral strategies under different environmental conditions, thus maximizing its fitness in a variable environment. This distinction is obviously related to the passive/active distinction: active plasticity is likely to be adaptive.

Phenotypic plasticity can be structured in various ways: it can be continuous or discontinuous, restricted to a brief developmental window or ongoing throughout the life of the organism, reversible or irreversible (Pigliucci 2001; West-Eberhard 2003; Whitman and Agrawal 2009). Some properties of organisms vary continuously with environmental factors: in many organisms, for example, size varies continuously with the temperature the organism experienced during its development (within certain bounds). Discontinuous variation can result when the organism possesses distinct alternative developmental pathways, separated by environmentally sensitive "switches": in alligators and some turtles, for example, sex is determined by the temperature in the nest early in the incubation process. A small difference in temperature can result in a different setting of the "switch" that determines whether the embryo will develop as female or male. This case is one of many in which divergent developmental pathways are accessible only at a particular developmental stage—temperature affects sexual differentiation only during a brief developmental window. There are also many cases, however, in which divergent pathways are accessible throughout the life of the organism. Clownfish begin life as males but can become female either early or later in life if no dominant female is present in the local environment. Some changes, like the clownfish's, are irreversible once they occur, but others (such as seasonal changes in mammals' coat color, birds' plumage, or plants' foliage) are readily reversible.

Most research on phenotypic plasticity focuses on morphological examples like these, but behavior is involved with plasticity in several different ways. Behavior itself—what Richard Dawkins called "the trick of rapid movement" (Dawkins 1976) could be seen as a form of very swift, highly reversible phenotypic plasticity. Larger patterns of behavior can be plastic at various scales or levels—they can be modified in various ways in response to environmental factors, as in psychological priming, imprinting, conditioning, and more sophisticated forms of learning. Developmental plasticity in animals can also involve aspects of neural and endocrine system development that may be developmentally locked in with lifelong effects on behavior. Rat pups neglected by their mothers, for example, grow up with more reactive cortisol systems, while rats raised in environments offering enriched sensory and cognitive stimulation grow up with thicker cerebral cortexes and denser neural networks; both changes continue to affect their behavior in adulthood. In other cases, such neural and endocrine changes may themselves remain plastic in varying degrees. Recent research on neuroplasticity, for example, has begun to reveal the remarkable ongoing adaptive capacity of many aspects of the brain's structure and function.

The evolution of plasticity has been a major focus of research in recent decades. Evolutionary theorists long discounted the importance of adaptive plasticity on the supposition that it was very difficult to achieve—requiring elaborately integrated mechanisms for detecting and responding to environmental conditions, which could evolve only in lineages exposed to reliably repeated environmental variations with distinct selective pressures—and so must be a rarity. But this conclusion has proven to be mistaken; adaptive plasticity is ubiquitous, as are the various particular adaptations that make it possible. In particular, nervous systems and endocrine systems—both crucial to human sex differentiation as well as to many of the other features of human nature emphasized by evolutionary psychologists—are adaptations *for* plasticity.

A few additional aspects of phenotypic plasticity are particularly worth noting. One is the way in which adaptive plastic responses are evoked. The environmental cue that triggers such a response is very often not identical with the environmental change to which the response is adaptive but is a proxy or indicator that the organism can detect more easily or earlier. This enables organisms to show anticipatory plasticity: adaptive changes that appear in advance of the environmental changes that select for them. Many seasonal changes in plants are adaptive to changes in temperature, precipitation, or pollinator presence, but plants often actually initiate such changes in response to changes in the amount of daylight, a (usually) reliable indicator of coming changes in the biologically significant variables. Often such changes are cued by the proxy variable's crossing a threshold, which means that small changes in proxy variables can sometimes trigger large changes in plastic characteristics or behaviors. In a famous case from horticulture, a large section of a greenhouse of poinsettia plants was prevented from blooming by the night watchman's habit of stopping at the same spot each night to light a cigarette: poinsettias begin their blooming cycle in response to the long nights presaging the rainy season in their home environment, and the brief flash of the watchman's lighter broke the night into two segments, neither of them long enough to trigger blooming. In other cases (where the threshold is not crossed) large changes in the proxy variable may have no effect at all on plastic phenotypes.

Finally, since proxies are important only because of their correlation with biologically significant variables, it is not always obvious what they are even if the adaptive function of the plastic response is known. The discovery that photoperiod-sensitive plants like poinsettias respond to seasonal changes in daylight was an important one, but the further discovery that they are responding to night length, rather than day length, took almost two more decades. Because animals have a far richer array of mechanisms for sensing environmental variation than plants do, identifying the proxies that animals use as cues can be very challenging.

Not only the proxies but some plastic responses themselves may be difficult to discover. Interesting recent work suggests that organisms may harbor considerable "latent" plasticity, some of it perhaps surviving from much earlier evolutionary periods—plasticity that is tapped very rarely if at all simply because the environmental triggers needed to elicit it occur rarely or never.

A final point worth special note is the complex relationship between phenotypic plasticity and phenotypic stability. Although plasticity is usually associated with change or variability, it can play a key role in producing stability or uniformity if the particular environmental factors to which a plastic response is linked are themselves stable or uniform. One important kind of case to consider here involves "scaffolds"—structures in the environment that serve as guides or templates for plastic developmental processes. The mature form of twining plants is determined by the structures about which they twine, for example, while the array of speech sounds that adult humans can distinguish in hearing is determined by the patterns of meaningfully different speech sounds they were exposed to as young children. The acquisition of particular concepts and bodily skills is similarly scaffolded by artifacts and cultural practices. The things we surround ourselves with—tools and toys, vehicles and weapons—shape our minds and capacities in ways that are sometimes passed from generation to generation for remarkably long spans of time (Sterelny 2012).

Plasticity can also play another role in producing stability by enabling an organism to respond differently to different external influences so as to reach or maintain a stable outcome despite environmental variability. The plastic response of individual branches allows a tree to arrive at the same overall mature form even if it loses limbs or must grow around obstacles; the plastic responses of the brain allow it to compensate for injury by recruiting other regions to perform functions normally executed by the damaged region. Most stability in living things is of this sort: robust rather than rigid; actively maintained and adjusted by plastic response in such a way as to compensate for perturbations rather than resulting from simple resistance to modification. Such robust stability is in fact essential to the operation of plasticity that is actively responsive rather than passively malleable. The alternative developmental pathways that endow an organism with active plasticity are themselves robustly structured, and their activation by environmental triggers is also reliably achieved despite other kinds of variability. Temperature-based sex determination offers a striking example. For a brief period, as we noted earlier, alligator embryos are highly sensitive to the temperature of their nests—which determines whether they will develop as males or females—but robust to other environmental variation. Once their commitment with regard to sex is made, however, the developmental process in either pathway is robust to further fluctuations in temperature. Another example is an equally striking case of conditional sexual strategies. Male Atlantic salmon have two different ways of reaching sexual maturity. Some fish grow to a large size (from fifty centimeters to a meter in length) and take a long time to reach maturity (up to seven years). Others mature at a very small size—as small as six centimeters—and reach maturity in less than half the time taken by the large fish. The large males (anadromous males) mature at sea, while the small ones (mature parr) are able to reach maturity without leaving the rivers where they were spawned. Which strategy a young salmon will follow is determined by his growth rate early in life—growth rates below a certain threshold trigger the process of early maturation. Different genotypes have somewhat different thresholds, but for each genotype the two developmental paths are robust once under way, even though tiny differences in early life can make the difference in which path a fish follows.

What are the implications of all this for thinking about human response functions? It is clear that sensitivity to environmental variability—especially to variability in social environments—and the capacity to respond plastically to it are enormously important to human beings. We are evolved for plastic response at many levels: developmental, behavioral, cognitive, and cultural. But much of the plasticity we possess is directed toward maintaining the stability of certain outcomes in the face of the enormously diverse physical, biotic, and social environments in which we find ourselves. Thinking about the role of plasticity makes clearer what we need to know in order to be able to draw conclusions about the shape of response functions. We need answers to these questions: Which phenotypic features are plastic, and what environmental proxies are they sensitive to and in what ways? Which features are robustly maintained and how? Uniformity of a particular characteristic does not show that it is not plastic since there are many reasons that available plasticity may not be in evidence. There is also reason to expect some apparently minor factors—proxies for biologically significant variables—to trigger strong responses. Some of these triggers (those affecting what I have called "biological levers" [Barker 2008]) may be capable of initiating causal cascades with far-reaching effects, as peoples' responses change their effects on others, triggering further responses and further environmental changes.