Has evolution primed humans to "beware the beast"?

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It has been a common premise in visual science that perception starts at the retina. According to this view, the retina is stimulated by light patches that provide information to the visual pathways and visual areas in the brain for analysis of spatial coordinates, movements, intensity, color, contours, and so on. Eventually these bottom-up processing steps meet with top-down driven expectancies to result in the construction of a percept that can be recognized and remembered. J. J. Gibson (1) radically challenged this premise by arguing that perception does not start at the retina but in the ecology, which through evolution has tuned perceptual processes to informational relationships in the environment. In his view, the task of perception is less to construct an image in the mind than to directly perceive richly informative, dynamic patterns of light beams emanating from objects and context in the environment, which provide affordances for action. Much in the ecological Gibsonian spirit, in this issue of PNAS, New *et al.* (2) provide a dramatic demonstration suggesting that the detection of changes in repeatedly presented pictures is driven by ancestral priorities rather than by current expertise.

Attention Priority for Animals

New *et al.* (2) argue that survival necessitated keeping an eye on animals (both human and non-human) in the ecology of evolutionary adaptiveness of the human species. For example, humans could turn out as potential mates, friends, or foes, and animals could signal a meal or a potentially deadly threat. Therefore, they argue, the human attention system evolved category-specific selection criteria to monitor animals (including humans) in the environment, which were automatic in the sense that they were relatively independent of context, goals, current state, and acquired expertise. New *et al.* tested this notion of evolutionarily driven attentional priorities in a change-detection paradigm derived from research on change blindness. Research participants were exposed to a long series of pairs of complex natural scenes that were rapidly alternated between versions showing just the scene and the scene plus an added object that was either animate (human, animal) or inanimate (plants or various artifacts including potentially moving ones such as vehicles). The results showed clearly superior performance in detecting humans and animals compared with all categories of inanimate objects that were tested. This effect, furthermore, could not be attributed to differences in size, contrasts, potential mobility, or confounds in terms of low-level visual features. Indeed, participants failed to detect (were "change blind" to) 34% of the added inanimate objects but missed only 11% of added animals or humans. Because of inferior performance in detecting vehicles, which not only can move but also are more prevalent and more dangerous than animals in the current ecology, New *et al.* argued that acquired expertise was not a factor in the superior performance in detecting animals. Rather, their data were taken to reflect an evolved mechanism of attention capture that gives priority to a highly relevant category of environmental stimuli in the ancient ecology of humans.

The human attention system evolved category-specific selection criteria to monitor animals.

These results extend previous findings suggesting faster detection of animals than other categories such as plants in a visual search setting (3, 4). These studies presented participants with different arrays of pictures, half of which showed pictures from the same category (e.g., flowers or mushrooms) and half of which had one of these stimuli exchanged for a target stimulus (e.g., an animal). The participants pressed different keys depending on whether a display contained a target or only showed distractors. Results from this paradigm show faster detection of a picture of an animal among pictures of plants than vice versa (3, 4). This convergence across quite different experimental paradigms is reassuring and strengthens the theory that an attentional priority for animals represents a genuine phenomenon.

Are All Animals Alike?

New *et al.* (2) took their findings as refuting a counter hypothesis of no categorical priming (which included a back-up hypothesis of priming rooted in acquired expertise). However, there are other interesting possibilities. One issue concerns whether animals provide a homogenous category or whether there are subcategories that are especially important in an evolutionary perspective. For example, it seems plausible that behavior systems for food foraging in predators would be tuned to detect prey with high precisions. Furthermore, given the survival contingencies of predation, it seems likely that perceptual systems for fast mobilization of defense would be tuned to quickly detect threat in potential prey. Indeed, LeDoux (5) has delineated neural circuitry that appears to achieve this purpose in the rodent brain. It involves a direct pathway via the thalamus that quickly activates the hub in the brain's fear network, the amygdala, which starts activating defense responses via connections to the hypothalamus and the brainstem even before the classic sensory cortices become involved. There is a bulk of evidence supporting a similar system in the human brain (6). This defense system can be grounded in a plausible evolutionary scenario, which supports that there might be an adaptive system focused on predators, and particularly snakes, in the primate family.

Snakes Shaped the Primate Brain

Isbell (7) proposed a theory that gives a pivotal role to snakes in shaping the mammalian brain because they were the only source of predatory pressure at two critical evolutionary junctures. First, constrictor snakes, which fed on the mole-like small nocturnal mammals destined to become primates, were the only available predators ≈100 million years ago. Thus, it is likely that the neural circuitry for defense behavior (the amygdala with associated input and output circuitry) originally was designed to deal with snakes and other reptiles rather than with attacking raptors or felines that were not around until ≈50

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million years later. Second, snakes with a very effective and potent venom delivery system appeared in Africa ≈60 million years ago. Because venomous snakes are often cryptic and difficult to detect, they provided a critical pressure to expand the visual system and integrate it with the fear system in the brains of anthropoid (i.e., monkeys and apes) primates. Isbell's theory (7) not only opens a new window on the evolution of the primate brain but also accounts for the differences in snake fears and visual systems in different primates. Old world monkeys, who display fear of snakes and have the most advanced visual system, remained in Africa under continuing pressure from snake predators. However, with the breaking apart of the southern supercontinent, Gondwanaland, lemurs evaded this pressure by dispersing to Madagascar, which lacks venomous snakes. And whereas the to-become new world monkeys reached and radiated through South America from the south, venomous snakes entered this continent much later and from the north (7). As a consequence, the contemporary descendents of primates who escaped venomous snakes by an early African exodus display less snake fear and more primitive and variable visual systems than their old world relatives.

There is a quite large literature that is consistent with a central role for snakes and other potentially dangerous small animals in human and macaque Pavlovian fear conditioning. Superior conditioning to snakes has been attributed to an evolutionarily derived preparedness to more readily associate fear with some objects rather than others (8). In the study that is most relevant for the present context, Cook and Mineka (9) demonstrated selective observational learning of fear in the rhesus macaque. Naïve, laboratory-reared monkeys were given the opportunity to see edited videos showing a conspecific displaying identical fear reactions to two different animals, a toy crocodile and a toy rabbit. Consistent with a large literature (8), the observer monkeys acquired fear to the potentially dangerous animal, the crocodile, but not to the more neutral rabbit, suggesting a readiness to associate fear with the animal signifying an evolutionary threat but not with a cute, nondangerous (and edible) animal.

Future Developments

Isbell's (7) theory, as well as the literature on preparedness and conditioning (8), suggests that there is an important distinction within the category of animals between those that have provided a recurrent survival threat in an evolutionary perspective and those that have not. This possibility was not examined in the research by New *et al.* (2), even though their method might provide a suitable tool for such a test by the inclusion of different categories of animals, some of which have been potentially dangerous in an evolutionary perspective. This is important because the data from visual search studies on this issue are not conclusive. Even though snake- or spider-fearful participants preferentially attend to their feared animal among other animals in a visual search setting (10, 11), claims that nonfearful participants more effectively detect evolutionary fear-relevant stimuli than neutral stimuli (e.g., ref. 10) can be questioned because they used inanimate plant objects (flowers and mushrooms) rather than nonthreatening animals as distractor stimuli. Indeed, one experiment that directly compared threatening and pleasant animals, as well as plants, as targets among a complex array of neutral objects reported faster detection of animals than plants but no difference in the detection of threatening and pleasant animals (3).

Visual search paradigms are notoriously sensitive to perceptual confounds in terms of low-level visual differences between target and distractors (e.g., ref. 12), which make them less than perfect tools for reaching definite conclusions about attentional guidance by the semantic content of visual categories. Because the change-detection paradigm used by New *et al.* (2) does not require direct comparison between simultaneously presented stimuli but the occurrence of a new stimulus in the context provided by the picture, it may more directly assess attention captures and be less susceptible to visual confounds than the visual search paradigm. The change-detection paradigm, therefore, is a potentially important tool for continuing analyses of the role of semantic categories and emotional stimuli in the capture of attention. Because the background scene sets the stage for detection, this method also allows the examination of the interesting question of whether the detection of added objects is context-dependent.

A larger issue concerns the framing of evolutionary arguments in the context of behavioral experiments. The argument of New *et al.* (2) is essentially a functional one, which elaborates the usefulness of a particular behavior in a back-projected "ecology of evolutionary adaptiveness" for ancestral hunter-gatherers. An alternative explanatory route, based on learning, could involve a connectionist network driven by a simple Hebbian rule, which, given the many ubiquitous characteristics of animals, would be likely to delineate a strong category that is distinct from other objects, including vehicles. During human ontogenesis, members of the animal category are likely to serve as stimuli in both appetitive and defensive conditioning episodes, the effects of which would generalize to the category as such, giving its members various degrees of attention-capture power.

A more complete evolutionary understanding (components of which could involve learning) would profit from careful analyses of the relevant ecology (1), considerations of brain circuitry and its evolution (5), and comparative perspectives attempting to trace evolutionary trajectories (7).

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