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Biases in signal evolution: learning makes a difference

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It is now well established that signal receivers have a key role in the evolution of animal communication: the suite of sensory and cognitive processes by which animals perceive and learn about their environment can have a significant impact on signal design. A crucial property of these information-processing mechanisms is the emergence of 'receiver bias' in the behavioural responses to signals. Whereas most research has focussed on receiver biases in the sensory system, more recent studies show that biases can also arise from learning about signals. Here, we highlight how learning-based biases can arise, and how these differ from biases emerging from sensory systems in their impact on signal evolution.

Signal evolution by receiver biases

A commonly held view is that signal evolution progresses through selection for costly signals that provide receivers with reliable information [1–4]. However, over recent years, this position has been eroded by studies showing that signal evolution can be driven by 'receiver biases' [5–10]. Receiver biases can be defined as byproducts of natural selection or as incidental non-selected consequences of the way in which sensory systems or brains are formed [4], predisposing receivers to respond more strongly to one signal than to another and even to prefer novel signals [9,10]. Here, we demonstrate that different types of receiver bias operate under different conditions and can have different implications for signal evolution. We focus on two opposite corners of what can be viewed as a continuous space determined by two different dimensions of the proximate mechanisms underlying receiver biases. The first dimension is whether biases result from the peripheral physiology of sensory systems or from higher cognitive brain processes. The second dimension is developmental phenotypic plasticity: some biases develop in the same way over a wide range of conditions, whereas others depend heavily on specific experience.

We differentiate here between 'sensory system biases' (see Glossary), which we define as receiver biases arising from more peripheral and primary sensory processing mechanisms and also showing limited if any phenotypic plasticity, and 'learning-based biases', which we define as arising from central information processing involving plasticity generated by learning. In making this distinction, we create a false dichotomy within a continuum. However, we do so to illustrate how different proximate mechanisms can differ in their impact on signal evolution.

Sensory system and learning-based biases

Perhaps the most well known and widely cited example of a signal that might have evolved owing to a sensory system bias is the 'chuck' component of the male mating call in the Túngara frog *Physalaemus pustulosus*. Results from comparative studies suggest that, before the chuck signal evolved, ancestral female frogs already had a bias in their auditory system to respond to particular sound features, which drove subsequent call evolution [5,6]. Other examples of traits that are likely to have evolved by exploiting sensory system biases are the swords of swordtail *Xiphophorus* fish [7,8], the vibratory signals of the water mite *Neumania papillator* [11,12], the red coloration of the male three-spined stickleback *Gasterosteus aculeatus* [13] and the blue and yellow coloration of two Lake Victoria cichlid species *Pundamilia pundamilia*

Glossary

Area shift: a phenomenon similar to peak shift where the peak response remains highest for the training stimuli but the generalization gradient is asymmetric, resulting in higher responses to novel stimuli away from the S^+ in the direction opposite from the S^- and vice versa.
Discrimination learning: the process by which animals learn to discriminate among stimuli, either along a single stimulus dimension or using more complex multidimensional features.
Generalization gradient: the degree to which an animal trained to respond to a particular stimulus will respond to novel stimuli that vary along a stimulus dimension shared with the training stimulus.
Intensity dimension: stimuli differ along an intensity dimension when they stimulate the same receptors but to a different extent; for instance, two lights of the same wavelength differing in intensity; chemical substances differing only in concentration; or tones differing only in amplitude.
Learning-based bias: a receiver bias that is generated through learning; for example, peak shift.
Peak shift: a consequence of discrimination learning between an S^+ (a positively rewarded stimulus) and an S^- (a negatively or neutrally rewarded stimulus) that differ along a stimulus dimension, leading to stronger responding to novel stimuli away from the S^+ in a direction opposite from the S^-, and vice versa (Box 1).
Rearrangement dimension: stimuli differ along a 'rearrangement' dimension when each stimulus addresses a different set of receptors, such as lights differing in wavelength; chemicals of different structure; or tones of different frequency. Whereas an intensity dimension can be considered a quantitative dimension, the rearrangement dimension is more qualitative.
Sensory system bias: a receiver bias arising from peripheral sensory processing. Although this need not imply absence of environmental plasticity, we assume here that it does.
Stimulus dimension: any aspect of a stimulus that can vary along an axis; for example, light intensity or angle of orientation.

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and *Pundamilia nyererei* [14]. These biases are assumed either to be byproducts of the sensory systems involved [7] or to arise in these systems as a result of selection for signal detection in other contexts. For example, the vibratory water movements in the water mite might have arisen from exploiting predator detection mechanisms [11,12], the red coloration of stickleback males might result from selection for preferences for red food items [13], and the blue and yellow colour in cichlids might be a consequence of a differential sensitivity to long and short wavelengths owing to adaptation to different ambient light conditions in both species [14]. Although we do not know whether these biases lack phenotypic plasticity, this is often implied from the finding that related species share similar biases and that the processing is peripheral. Here, we assume that they have limited plasticity.

Learning-based biases arise from the cognitive mechanisms that process and store information. There is an increasing awareness that biases based on cognitive processes could be just as important for signal evolution as are sensory system biases [15–25]. Not all biases arising from cognitive processing are necessarily plastic. However, most interesting from our perspective are biases that arise from the way in which animals learn to recognize important environmental features. One mechanism that can generate a learning-based bias is that of 'peak shift', which emerges from learning to discriminate among stimuli [26,27]. Using peak shift as an example, we highlight the need to consider sensory system and learning-based biases as distinct selection pressures in signal evolution.

Learning and generalization

In many contexts, responding to signals involves learning. Avian predators, for instance, avoid prey with aposematic warning signals by learning to associate the coloration with the defences (e.g. Ref. [28]), songbirds learn to recognize the songs of conspecifics or local geographical variants of songs (e.g. Ref. [29]), and bumble bees learn to recognize the colour of the most profitable flowers [30]. Recognition involves remembering particular signals, but also discriminating them from other similar signals. Thus, predators can learn to discriminate between undefended and defended prey using visual patterns, songbirds learn to ignore the songs of other sympatric bird species, and bumble bees learn to avoid the colours of less profitable flowers. This discrimination learning process also determines how animals respond to novel stimuli; that is, how they generalize (e.g. Refs [26,27,31–33]).

Generalization gradients resulting from discrimination learning have been extensively studied by psychologists in experimental laboratory settings, often using simple artificial stimuli, such as tilted lines, lights of different wavelengths or tones of different frequency (e.g. Refs [26,27,31–34]). In these experiments, animals are usually trained to discriminate between two stimuli that are differentially reinforced, where one stimulus indicates the presence of a reward (S^+), and the other stimulus is neutral or indicates some punishment (S^-). After training, animals are presented with novel stimuli that differ from their training stimuli to varying degrees, and their responses are measured. Although we might expect that the strongest responses are seen towards the training stimuli, this is not always the case, and the strongest response might be given to stimuli that are more extreme on the dimension separating the training stimuli (Box 1). This shift in generalization gradient is known as a 'peak shift' because the peak response is shifted along the training dimension away from the original stimuli used in training. The shape of this generalization gradient differs depending on whether the training stimuli vary along an 'intensity' dimension (e.g. two lights of the same wavelength differing in intensity) or qualitatively along a 'rearrangement' dimension (e.g. two lights of the same intensity but of a different wavelength) (Box 1).

A less extreme version of peak shift is 'area shift', where, although the peak response remains highest for the training stimuli, the generalization gradient is skewed, with novel stimuli on the S^- side of S^+ receiving fewer responses than S^+ and novel stimuli on the other side of S^+ getting similar responses as S^+ [34,35]. Apart from peak and area shift, other types of generalization processes can also bring about preferences for novel stimuli, such as 'range effects' (e.g. Ref. [34]), in which the location of the peak in responding depends on the range of stimuli used in testing. However, the relevance of these processes to signal evolution is still unclear.

Peak shift is an example of a learning-based bias that can drive signal evolution. It is taxonomically widespread, occurring in vertebrates and invertebrates, and appears to be a general property of discrimination learning. Peak shift is also found for a range of different stimuli in different sensory modalities (e.g. vision, hearing or olfaction), and along many perceptual dimensions (e.g. such as the frequency, duration or amplitude of a sound signal). It is a fundamental property of discrimination learning; therefore, whenever animals learn to discriminate among closely similar signals, whether prey coloration, conspecific song, or floral colours, they might develop biases that can select for more extreme signals. However, does peak shift occur in more biologically relevant contexts similar to the ones the animal has to solve in every day life, or with more complex stimuli compared with the tilted lines or coloured keys found in traditional experimental psychology experiments?

Peak shift in the natural world?

There is increasing evidence for peak shifts in a more natural context. One example of this concerns a task that humans perform in daily life: face recognition. Humans show peak shift when they have to distinguish similarly looking faces [35]. This is also thought to give rise to the phenomenon where we are better at recognizing familiar individuals from caricatures exaggerating specific features than from drawings based on real facial features [36]. For animals, several recent studies have also used complex stimuli that either are close to natural ones or are biologically relevant, for instance using a learning task that is more similar to one they are likely to experience in the wild. Peak shift has, for example, been observed in the spatial orientation of pigeons *Columbia livia* and honey bees *Apis mellifera* in relation to artificial 'landmarks' [37,38], while sphinx moths *Manduca sexta*, which use