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Department of Neuroscience, University of Connecticut Medical School, Farmington, Connecticut 06030, USA.  
E-mail: pfeiffer@neuron.uhc.edu

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## Cognition and Evolution: Learning and the Evolution of Sex Traits

The evolution of gender characteristics is an outcome of mate choice, which has been assumed to be genetically mediated. Recent research suggests that learning also has a role to play as an agent of sexual selection.

Spencer K. Lynn

Many animals, some birds being well known examples, exhibit conspicuous appearance (e.g., bright, colorful plumage or extravagant tails) at some cost (e.g., attracting predators). Models for the evolution of such traits have posited strong genetic links between expression of the trait, e.g., by males, and preference for the trait, e.g., by females exercising mate choice. The traits are considered to be indicators of Darwinian fitness and the preferences are thought to be unlearned [1].

Sexual imprinting, exhibited by many animals, including humans [2], is one exception. Imprinting refers to a form of learning confined to a sensitive period at the beginning of an animal's life. Preferences are established by exposure to parental traits shortly after birth. Those preferences show later, in the young adult, when the animal makes choices about whom to court. On the surface, however, imprinting alone was not thought to drive a preference for traits different from those expressed by the parents. Instead, some form of inflexible perceptual bias was thought to be required to drive

selection for exaggeration of imprinted traits [3–6].

However, recent research indicates that an outcome of discrimination learning, known as 'peak shift', may couple learning to

the evolution of trait exaggeration. Peak shift is a behavioral phenomenon arising from discrimination learning and has become one of several topics in psychology taken up by behavioral ecologists seeking to bridge learning and decision-making to the evolution of cognitive abilities. In particular, peak shift has been implicated in the evolution of signaling systems. Theoretical studies have explored the potential role of peak shift in the evolution of gender or species recognition characters, warning coloration and

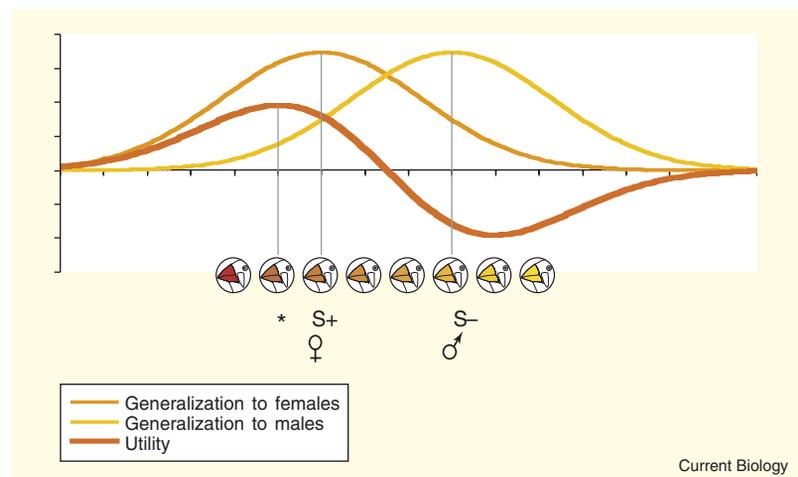


Figure 1. Peak shift is a directional preference for novel stimuli characterized by aversion to the risk of stimulus misidentification.

In this illustration, after the experiment by ten Cate *et al.* [13], male zebra finch chicks learn what adult males and females look like by imprinting on their parents (S+, maternal beak color, and S-, paternal beak color). Later, as young adult birds, the males are allowed a choice of females to court (eight beak colors). The males generalize what they have learned about their parental beak colors to similar beak colors (bell-shaped generalization curves). When these generalizations overlap, uncertainty ensues about the outcome of responding to stimuli: any given beak color might indicate a male or a female. How should a young bird decide who to court? Response strength (e.g., amount of courtship behavior) can be described by a utility function (Box 1). The utility function exhibits peak shift, predicting that a bird with a somewhat redder beak than the mother (asterisk) will be courted more vigorously than one with the mother's beak color, as shown by the ten Cate *et al.* experiment [13].

Box 1

The utility function explaining occurrence of peak shift.

In the experimental setting used by ten Cate *et al.*, response strength is influenced by three parameters, described by straightforward algebra:

$$U(x) = [\alpha h f_{S+}(x_i) + (1 - \alpha) a f_{S-}(x_i)] - [\alpha m f_{S+}(x_i) + (1 - \alpha) j f_{S-}(x_i)]$$

$U(x)$  is the utility, or relative benefit, of courting a bird with a given beak color,  $x_i$ , less the utility of withholding response to that bird. The first parameter influencing response strength corresponds to the range of beak colors over which males and females are presumed to vary, represented by  $f_{S+}(x_i)$ , the relative frequency of a particular beak color  $x_i$  from the distribution S+ (females), and  $f_{S-}(x_i)$ , the relative frequency of a beak color  $x_i$  from the distribution S- (males). The second parameter is the relative probability of encountering females,  $\alpha$ , and males,  $1 - \alpha$ . The third parameter is the relative payoff accrued for responding to or ignoring S+ and S- stimuli. The payoffs are  $h$ , the benefit accrued for responding to S+ (e.g., a chance to produce offspring);  $j$ , the benefit of not responding to S- (e.g., time and energy not wasted courting the wrong gender);  $m$ , the cost of not responding to S+ (e.g., lost mating opportunities); and  $a$ , the cost of responding to S- (e.g., time and energy wasted courting the wrong gender).

The risk of a misidentification mistake is compounded by overlap of the generalization distributions, increased relative frequency of S- (low  $\alpha$ ), and large relative cost terms ( $m$ ,  $a$ ) [14], each of which serve to increase the magnitude of the peak shift [7].

sexually dimorphic exaggerated traits [7]. Experiments have shown that peak shift can drive signal evolution in warning coloration and mimicry systems [7–8].

Imagine the following result, a common finding in discrimination learning experiments [9]: Control subjects are trained to respond to stimulus ‘S+’ (e.g., a color of a particular hue). Treatment subjects are trained identically to control subjects with respect to S+ and are also trained to withhold response to ‘S-’ (e.g., a slightly different hue). When tested on a continuum of stimuli, the control subjects’ peak response strength is at S+, as one would expect. However, the treatment subjects’ maximal response is shifted relative to that of controls to a never-before-seen and unrewarded stimulus. This behavior exhibited by treatment subjects is peak shift. A plot of response strength as a function of stimulus value shows a pulse-shaped curve. The peak of response strength is shifted off of S+ in a direction away from S- [9]. There is a reciprocal shift of the most strongly avoided stimulus off of S-, away from S+ [10].

The seemingly paradoxical preference for a novel

stimulus — and one somewhat extreme or exaggerated relative to training stimuli — can be understood as a mechanism for minimizing the risk of responding to the wrong stimulus under conditions of uncertainty (Figure 1). This phenomenon is of interest for several reasons. One point of interest is that preferences are being learned in the absence of the preferred stimuli and are shaped by the presence of unpreferred stimuli. The biological mechanisms of this preference establishment are poorly described. Moreover, peak shift is taxonomically widespread, exhibited by pigeons; rats; primates, including humans; fish; moths; and bees [7,11–12]. The phenomenon thus appears to reflect universal attributes of generalization, discrimination learning and choice-making behavior. Lastly, peak shift has been recognized as a possible influence on the evolution of animal communication signals [7]. Cognitive motivations for behavior may thus have a role as a selective mechanism driving evolution, in addition to the better known interactions between genetic and environmental factors that form the basis of natural selection.

In this issue of *Current Biology*, ten Cate, Verzijden, and Etman [13] use the zebra finch to show that peak shift exhibited during courtship can arise from imprinting on parental appearance. Despite the steady interest in peak shift over several decades, there is one of very few experiments actually putting peak shift into an ecologically valid context (i.e., utilizing naturalistic designs for stimulus learning and choice), and the first to show that peak shift can arise from imprinting and has the potential to drive the evolution of gender-diagnostic characteristics. In the experiment of ten Cate *et al.* [13], male zebra finch chicks were imprinted on the beak color of their parents as a way to distinguish males from females (Figure 1). Beak color was manipulated with paint. Some chicks were raised with red-beaked mothers and orange-beaked fathers. For other chicks the colors were reversed. Later, as young adults, the chicks made choices about which of several females to court. The females differed by beak color, which spanned an orange to red continuum, from more extreme than the paternal color to more extreme than the maternal color. The maternal beak color was thus considered S+ (eliciting response) and the paternal color S- (to be ignored). The chicks exhibited peak shift, i.e. they showed a preference to court females with beak colors shifted off that of their mothers in a direction away from that of their fathers (Box 1). Part of the significance of this study is that a preference was established for the exaggeration of a trait that was sex-linked yet the design of the experiment provided assurance that neither the trait nor the preference for it carried the genetic associations called for by conventional models of sexual selection. Beak color carried no inherent fitness advantage, did not communicate the possibility of ‘good genes’ to mates, nor would it impart a competitive advantage to future offspring who might possess it. Furthermore, the preference for the exaggeration was not genetically predisposed or based on a sensory bias, but learned and arbitrary (a shift was obtained

whether the maternal beak was orange and the paternal red, or vice versa).

There are a few important aspects missing from studies of the role of peak shift in evolution. ten Cate *et al.* [13] have done very well to use complex stimuli (living birds) in the learning and choice phases of their experiment. Yet, even so, the birds differed from one another on only one prominent dimension. Future research will need to examine if and how peak shift operates as stimulus complexity scales up to compound or multimodal stimuli, and if peak shift occurring over a subtle difference, such as beak color, remains influential on decision-making in the presence of more discriminative stimuli, such as overt plumage differences. As well, to date studies have examined only behavior in the initial generation of signalers and receivers. Evidence of directional evolutionary genomic change in the subsequent generation of signalers and a preservation of the directionality of learned preferences in receivers has yet to be sought. Imprinting is a special kind of learning. Conventionally, learning involves

some explicit payoff of reward or punishment accrued during trial and error. In imprinting such is not the case; payoffs are pre-organized. The mechanism of that pre-organization, and how it is accomplished evolutionarily and developmentally is not understood. One additional point of significance of the ten Cate *et al.* study [13], then, is that it indicates that peak shift might be used as a probe to investigate the mechanisms behind such pre-organized parameter specification.

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Harvard Medical School, Cognitive Neuroscience Laboratory, McLean Hospital, NB-G21, Belmont, Massachusetts 02478, USA.  
E-mail: [slynn@mclean.harvard.edu](mailto:slynn@mclean.harvard.edu)

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