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## Article

# Evaluation and hedonic value in mate choice

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## Abstract

Mating preferences can show extreme variation within and among individuals even when sensory inputs are conserved. This variation is a result of changes associated with evaluative mechanisms that assign positive, neutral, or negative hedonic value to stimuli—that is, label them as attractive, uninteresting, or unattractive. There is widespread behavioral evidence for differences in genes, environmental cues, or social experience leading to marked changes in the hedonic value of stimuli. Evaluation is accomplished through an array of mechanisms that are readily modifiable through genetic changes or environmental inputs, and that may often result in the rapid acquisition or loss of behavioral preferences. Reversals in preference arising from "flips" in hedonic value may be quite common. Incorporating such discontinuous changes into models of preference evolution may illuminate our understanding of processes like trait diversification, sexual conflict, and sympatric speciation.

Key words: associative learning, assortative mating, mating preference, sensory biology, valence

*How the sense of beauty in its simplest form—that is, the reception of a peculiar kind of pleasure from certain colors, forms, and sounds—was first developed in the mind of man and of the lower animals is a very obscure subject. The same sort of difficulty is presented, if we inquire how it is that certain flavors and odors give pleasure, and others displeasure. Habit in all these cases appears to have come to a certain extent into play; but there must be some fundamental cause in the constitution of the nervous system of each species.* (Darwin 1872, p. 414)

## Introduction: Sensory and Evaluative Processes in Mate Choice

### Sensory exploitation, sensory drive, and mating preferences

As amply shown in the other contributions to this volume, sensory perspectives on the evolution of communication have yielded one of the great successes of integrative biology. Two people, Mike Ryan and John Endler, deserve much of the credit for rescuing Animal Behavior from its fling with Dr Pangloss, by restoring the field to its mechanistic roots. "Sensory drive," as originally formulated by

Endler (1992), built on Ryan's (1990) "sensory exploitation" hypothesis that pre-existing sensory mechanisms exert selection on communication signals. Endler (1992) posited that receivers and signals evolve under selection to optimize transmission and detection in the sensory environment. Although these hypotheses apply to communication in a broad range of contexts, both these authors and the workers that followed them have focused largely on mating signals and mating preferences. A primary contribution of the focus on sensory systems has been to overturn the ever-resilient conventional wisdom that preferences must confer adaptive benefits to choosers. Sensory perspectives have shown that elaborate traits can evolve and diversify largely as a function of constraints on the mechanisms underlying preferences, and more generally have provided a unifying, integrative framework for studying behavioral evolution. It is powerful and satisfying to go from the amino acids underlying wavelength sensitivity (Boughman 2002; Seehausen et al. 2008), or the inner-ear morphology shaping frequency tuning (Ryan and Rand 1990), to the behavioral decisions underlying fitness variation and gene flow in the wild.

Yet the spotlight on sensory systems has led us to neglect some fundamental aspects of the mechanisms shaping mating decisions. As in the above examples, mechanistic studies of sensory drive and

sensory exploitation have focused overwhelmingly on the sensory periphery, and have largely supported Ryan and Rand's hypothesis that "[sexual] selection favors those traits that elicit greater stimulation from the female's sensory system" (Ryan and Rand 1990). Within some set of parameter values, this is always going to be true, because courters only have the opportunity to be chosen as mates if they are detected to begin with. And sensory systems are inevitably important to mate-choice evolution, because a chooser's sensory system determines the range of signals she can detect and influences the effective distribution of those signals from her point of view, which in turn affects how costly it is to sample potential partners (Dawkins and Guilford 1996; Rosenthal 2017). The trend in empirical studies likely continues to follow that shown by Ryan and Keddy-Hector (1992), that choosers overwhelmingly prefer stimuli that provided more sensory stimulation.

The sensory periphery is, of course, only the first in a host of mechanisms that shape mate choice. Within populations, the sensory periphery often explains little of the variation in behavioral preferences and less of the variation in mating outcomes (Fuller et al. 2010; Coyle et al. 2012). The catch-all term "chooser biases" (Rosenthal 2017) encompasses all mechanisms that bias mate choice but have not evolved in response to selection on mating outcomes. Sensory biases are the most basic form of perceptual biases (Ryan and Cummings 2013) that shape preferences but are not primarily shaped by selection on their function in choosing mates. Many of these perceptual biases, like the ones favoring optical illusions in bowerbird decorations (Kelley and Endler 2012) fit neatly into the framework of sensory drive and sensory exploitation: in attractive bowers, the constant texture gradient provided by forced perspective putatively increases the apparent size of display ornaments. But how and why do female bowerbirds come to prefer larger objects? More generally, how do choosers translate conspicuousness into preference, and why do they often ignore traits or prefer traits that confer less sensory stimulation?

As detailed in a recent review by Ryan (2018), mating decisions are quite typically complex and nonlinear. In particular, Ryan calls attention to phenomena like perceptual gating, detailed below, and comparative evaluation (Lea and Ryan 2015), both of which elicit preference patterns that cannot be explained purely in terms of sensory stimulation. These properties of mate choice require us to go beyond sensory stimulation, and return to Darwin's question about how choosers label stimuli as "good" or "bad"—that is, how they perform the task of *evaluation*. Yukalov and Sornette (2016)'s recent model provides a good fit to Lea and Ryan's (2015) demonstration of the so-called "decoy effect," whereby an irrelevant option changes the direction of preferences. Their model borrows from quantum theory to incorporate unobservable "irrational effects describing the attractiveness of choice." But although quantum entanglement may provide a useful metaphor for simulating the underlying dynamics, evaluative mechanisms are observable and can be modified through experience and selection. In some cases, these mechanisms approach the simplicity and accessibility of the sensory periphery. Understanding the process of evaluation is likely a key to addressing some of the key enduring questions of sexual selection and mate-choice evolution.

## Evaluation and sensation as distinct processes in mate choice

It is useful to consider evaluation as a distinct process from sensation when we study mate choice. Evaluation is a universal part of mate choice or of any behavioral decision, and operates in different ways and under different constraints than sensation. Both theoretical models and empirical research programs could benefit from the same mechanism-centered approach on evaluation that has been brought to bear in sensory exploitation and sensory drive.

As detailed below, examples abound of choosers preferring stimuli that elicit *less* sensory stimulation, and individuals vary in their preferences despite a conserved sensory periphery. In the extreme case, a stimulus can elicit preference in some circumstances and what Darwin called *antipathy* in others. In other words, the same sensory inputs are *evaluated* differently in the brains of receivers. Evaluation determines the mapping of sensory inputs, and perceptual inputs more generally, to appetitive and aversive behavioral responses (Berlyne 1970; Ellingsen et al. 2015). We can assign *hedonic value*, which can range from positive to negative (Berlyne 1970), to stimuli as a function of how they affect a courter's probability of mating with a given chooser (Rosenthal 2017).

Just like sensory biases, the mechanisms involved in evaluation can evolve in response to ecological selection, changing how mating preferences are expressed; alternatively, they can act to decouple preferences from ecological constraints on sensory function. Through processes like associative learning, evaluation is highly labile even within a chooser's adult life. And work in a range of taxa suggests that evaluative mechanisms can yield qualitative "flips" in preference, with important consequences for sexual selection, sexual conflict, and reproductive isolation. Here, in the spirit of Ryan (1990) and Endler (1992), I suggest a simple conceptual framework we can use to think about the role of evaluative mechanisms in shaping mating preferences.

## Evaluative mechanisms: illustrative examples in frogs and moths

Two case studies are instructive in helping us think about evaluative mechanisms in an evolutionary context. In the first, sensory inputs are filtered by a process called perceptual gating. In túngara frogs *Physalaemus pustulosus*, as in many species, females respond to a far narrower range of cues than males. Hoke and colleagues (Hoke et al. 2008, 2010) played a range of calls to males and females and then used immediate-early-gene expression as a proxy of neural activity. They found that sensory inputs were conserved: male and female auditory brainstem showed similar, indiscriminate response. In contrast, females and males were divergent in the torus semicircularis, a region of the auditory midbrain that relays sensory input to motor activity. Although the torus of males responded to a range of calls, in females it only showed activity in response to conspecific calls, mimicking females' behavioral preferences. The torus semicircularis therefore acts as an evaluative mechanism—a "gatekeeper" (Hoke et al. 2008) that determines whether stimuli elicit motor activity or whether they are ignored. In songbirds, evidence suggests a "gatekeeper" role for both the high vocal center (HVC; Brenowitz 1991; Riters and Teague 2003) and catecholamine pathways in the ventromedial nucleus of the hypothalamus (VMH; Riters et al. 2007; Pawlisch and Riters 2010; Riters et al. 2013).

Like male and female túngara frogs, males of the E- and Z-strains of the European corn borer moth *Ostrinia nubilalis* share a conserved sensory periphery. Yet males are attracted to the pheromone blend of females from their own strain, and inhibited from approach by the pheromones of the other. This is accomplished by an elegant system early in neural processing. In the E-strain, E-sensitive olfactory neurons project into the medial glomerulus, eliciting approach behavior, and Z-sensitive neurons project into the lateral glomerulus. The pattern is reversed in Z-strain males (Kárpáti et al.

| Strain | E | E | Z | Z |
|---|---|---|---|---|
| Pheromone blend | E: z | ε: Z | E: z | ε: Z |
| Odorant receptor neuron | E Z | E Z | E Z | E Z |
| MGC glomeruli | | | | |
| Hedonic value | + - | + − | + − | + - |
| Behavioral response | + | - | - | + |

**Figure 1**. Schematic outlining reversal of hedonic values for the E: Z ratio of pheromone blends in E- and Z-strain males of *O. nubilalis*. For both strains, neurons responding to the strain's own major pheromone project into the medial glomerulus and neurons responding to the minor pheromone project into the lateral glomerulus (Kárpáti et al. 2008). After Rosenthal (2017).



**Figure 2**. Evaluative mechanisms lead to different behavioral responses as a function of sensory stimulation, in this case detection of a nonvolatile odorant by a hypothetical mammal. Under preference (green), sensory stimulation is assigned a positive hedonic value, leading to behaviors that increase the probability of mating. With indifference (white), sensory inputs are ignored, producing no behavioral response. With antipathy (red), sensory stimulation leads to behaviors that decrease the probability of mating. Mammal drawing by Carmen Rosenthal Struminger.

2008; Figure 1). In these moths, therefore, reversal in behavioral preference is thus the consequence of a reversal in neural wiring that integrates inputs from the sensory periphery. Molecular-genetic studies in other insects suggest that such a reversal can be induced by a simple genetic change. In the silkmoth *Bombyx morii*, a similar reversal in axon targeting can be produced by disrupting the activity of a single transcription factor, *Bmacj6* (Fujii et al. 2011). Similarly, alternative splicing of the *fruitless* transcription factor in *Drosophila melanogaster* causes a "flip" in axon targeting responsible for attraction versus avoidance of male pheromone cues (Kimura et al. 2005). In each of these cases, a change in a single gene causes complete reversal of the hedonic value assigned to a stimulus, apparently without affecting sensory processing. In corn borer moths, the E-strain scent is labeled "good" in E-strain males, and "bad" in Z-strain males—and vice versa for Z-strain scent.

The torus semicircularis of túngara frogs and the wiring of olfactory neurons in insects are therefore examples of evaluative mechanisms. They differ in that the former regulates whether or not a stimulus elicits a behavioral response, the latter what kind of behavior is elicited. They share the important properties that 1) they can vary with marked consequences for behavioral preferences even when sensory processing is conserved; and (2) extreme differences in preference can arise as a result of discrete endocrinological or genetic modifications. As I will return to, a number of studies have shown that social or environmental effects can do the same.

## Evaluation: an extremely simple model

Evaluation is implicit in the process of mate choice, which requires making a behavioral decision as a function of signal value. We can represent this in a minimal computational model of mating preferences, defined following Heisler et al. (1987) and Jennions and Petrie (1997) as "a chooser's internal representation of courter traits that predisposes her to mate with some phenotypes over others" (Rosenthal 2017). The output of this minimal model, connecting a single sensory input with a single evaluative mechanism, is represented in Figure 2. Under a purely sensory view of mate choice, sensory stimulation elicits neural, physiological, and behavioral changes that increase the probability of mating: stimuli always have positive hedonic value (green). But evaluative mechanisms can also act to filter sensory stimulation, such that it fails to elicit a sexual
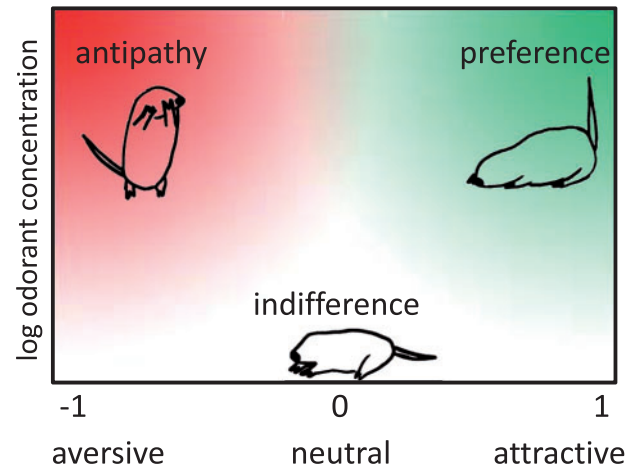
response (indifference, white), as with heterospecific calls filtered by the torus semicircularis of female túngara frogs. Finally, stimuli can elicit what Darwin (1871) termed antipathy (red), as in the targeting of Z-strain odorant receptors in E-strain *Ostrinia*. Evaluation can thus affect peak preference (the value most preferred by choosers) as well as choosiness or strength of preference (the extent to which one value is preferred over others; Rosenthal 2017).

Just as it is useful to think about sensation in terms of stimulus conspicuousness, it is useful to think about evaluation in terms of a stimulus' hedonic value. Conspicuousness can be measured using conditioned-response assays, neurophysiology, or physical modeling; similarly, hedonic value can be assayed in terms of neural, physiological, and behavioral responses. A stimulus with a positive hedonic value is attractive: it elicits arousal and proceptive behaviors like approach and sexual displays. A stimulus with a negative value is aversive, eliciting avoidance and inhibiting arousal. The notion of hedonic value is central to everyday experience across contexts: our environment is full of pleasant and unpleasant stimuli we experience fully, and of things we sense but do not pay attention to. It is intuitive that where things fall along this continuum is often quite labile: sautéed snails, beards, and reality-show politicians can be valued at opposite extremes even among full siblings.

It is straightforward to think of hedonic value as a scalar coefficient varying positively with the ratio of positive to negative responses, and ranging from −1 (maximally aversive) through 0 (utterly disregarded) through 1 (maximally attractive). Therefore,

$$\text{Preference } = \eta f(s),$$

where f(s) is a sensory response function and $\eta$ (from Greek ηδονική, hedonic) is the hedonic value coefficient. A useful analogy is the social interaction coefficient $\psi$, which determines the strength and sign of the effect of social experience on phenotypes. In Bailey and Zuk's (2012) study of field crickets *Teleogryllus oceanicus*, $\psi$ varied; experience with male songs had opposite effects on female choosiness in different populations. As with $\psi$ both the magnitude and the sign of the

coefficient $\eta$ are important; the magnitude determines whether choosers attend to the display traits they sense, and the sign determines whether they respond positively or negatively to these traits. I address the functional relationship between hedonic value and $\psi$ below.

If sensory stimulation is held constant, a chooser is more likely to mate with a courter expressing stimuli of higher hedonic value. In some cases, a chooser might well only have opportunities with $\eta < 0$. As Darwin (1871, p. 273) noted, a female "may accept, as appearances would sometimes lead us to believe, not the male which is the most attractive to her, but the one which is the least distasteful." In such cases, the "preferred" mate might be the one who elicits the least effort from choosers in terms of avoidance.

The simple model presented above may provide a useful heuristic for thinking about the evolutionary importance of evaluative mechanisms. It dramatically oversimplifies the interactions among perceptual nonlinearities, previous experience, and internal state that shape evaluative responses. Notably, a given stimulus can often exhibit change in hedonic value as a function of its intensity: the aromas of perfumes and cheeses provide a familiar example. Azanchi et al. (2013) showed that just as different sensory inputs can target populations of neurons leading to positive and negative responses, so too can different intensities of the same stimulus. Female *D. melanogaster* prefer oviposition substrates with low, but nonzero, concentrations of alcohol. This preference is achieved by a balance between "appetitive" populations of neurons activated at lower concentrations, and "aversive" neurons triggered by toxic concentrations.

At the behavioral as well as the neural level, it may be unwise to compress appetitive and aversive responses into a single scalar. Huxley(1966), observing intense courtship between birds, suggested that the complexity of mating displays was guided by the tension between appetitive and aversive responses. The same stimulus can elicit a mix of aversive and attractive responses within the same individual. A remarkable example comes from rats infected with the protozoan parasite *Toxoplasma gondii* (House et al. 2011). In uninfected rats *Rattus norvegicus*, the odor of female conspecifics is attractive, eliciting approach and proceptive behavior, whereas the odor of cat urine is aversive and elicits avoidance. *Toxoplasma*-infected rats, in contrast, are attracted by the odor of cats, *Toxoplasma*'s final host. Infected males exposed to cat urine show the same neural activity patterns as uninfected males in brain regions associated with fear and avoidance, but show similar patterns of sexual arousal as when responding to females; attraction overcomes fear. In the context of mate choice especially, it would be useful to consider evaluation in the context of competing appetitve and aversive responses.

## Sources of Variation in Hedonic Value

### Genetic variation in evaluative mechanisms

There is abundant behavioral evidence for extreme variation in hedonic value independent of variation at the sensory periphery, and a growing body of work has identified specific neural mechanisms involved in evaluation. In addition to the interspecific examples discussed above, choosers within a species can show genetic variation in the hedonic value assigned to stimuli. For example, the visual periphery is highly conserved within and between species of estrildid finches (Hart et al. 2000). Despite sharing the same sensory biases for color, female Gouldian finches *Erythrura gouldiae* prefer males of their own color morph. These preferences are robust to cross-fostering, and variation in preferences is associated with the Z chromosome inherited from fathers (Pryke 2010). Different Z-linked genotypes therefore assign different hedonic values to different morphs. The mechanism of

hedonic assignment is unknown: under the minimal model presented above, chromatic signals encoded in the retina could be sufficient to elicit positive or negative responses, but it is perhaps more likely that sophisticated integration of spatiotemporal cues (Rosenthal 2007) is recruited in distinguishing the morphs.

Evaluative mechanisms, like sensory mechanisms, can evolve. Some of the most straightforward demonstrations of preference evolution independent of sensory mechanisms come from preferences associated with body or ornament size: all else equal, larger objects stimulate a larger area of the retina. Wilkinson and Reillo (1994) selected on the length of the sexually-dimorphic eyestalk in male stalk-eyed flies to test for correlated evolution of preferences. Long stalks are a priori more detectable. Females in control lines and lines selected for long stalks both preferred long-stalked males, but females in the short-stalk-selected line preferred the males with the shortest stalks. Such a rapid reversal in response to selection may account for heterogeneity in preferences at a phylogenetic scale. In the poeciliid fish genus *Xiphophorus*, the preference for longer swords—pigmented elongations of the caudal fin—has been weakened (Basolo 1998), lost (Rosenthal et al. 2002), or reversed (Wong and Rosenthal 2006) in different lineages despite an ancestral bias for large apparent size. Intriguingly, the preference for swords is labile despite a conserved preference for larger body size. This suggests that in addition to changes in evaluation (swords are attractive to female *X. maculatus* but unattractive to *X. birchmanni*, neither of which sport swords), females have evolved the ability to perceive swords as distinct from total body size (Rosenthal and Evans 1998).

### Experience-dependent reversals in hedonic value

Choosers across vertebrate and invertebrate taxa show preferences that can be markedly modified by experience. These experiences range from lifetime effects on early development to short-term effects during the course of courtship interactions. In some cases, the effects of experience can be directly linked to sensory modification, for example the differential regulation of odorant receptors in response to olfactory exposure (Nevitt et al. 1994). In many more, such an increase in peripheral sensitivity to a familiar stimulus cannot be ruled out. Nevertheless, there are perhaps even more cases where we can be confident that an experience-dependent preference involves a change in hedonic value against the background of a conserved sensory response. This is the case for sexual imprinting in zebra finches, where individuals develop preferences for stimuli found in the opposite-sex parent and antipathies for those found in the same-sex parent (ten Cate et al. 2006). In a variety of species, exposure to danger, like predator cues, causes choosers to lose or reverse their preferences for ornaments providing greater sensory stimulation (Berglund 1993; Pilakouta and Alonzo 2014). A similar effect occurs in mate copying, where females prefer a previously unattractive male when he is paired with proceptive cues from another female (Mery et al. 2009; Vakirtzis 2011; Santos et al. 2014). Choosers often modify their preferences with age in ways unlikely to arise from sensory changes. For example, female satin bowerbirds are startled by high-intensity courtship displays when young, but prefer vigorously courting males when older: the more conspicuous stimulus flips from aversive to attractive presumably as a consequence of females learning to distinguish courtship from threatening stimuli (Coleman et al. 2004).

### Associative learning

Associative learning provides a final and ubiquitous pathway for assigning hedonic value to stimuli. Put simply, arbitrary stimuli that are

associated with good experiences in the context of mate choice become attractive, those associated with bad experiences become unattractive. For example, Coria-Avila et al. (2005) found that females learned to prefer an arbitrary odor applied to male rats in the context of "paced copulation," where females could control mating rate, but not in an "unpaced" context where females had to fend off mating attempts. So-called sexual reward—stimuli with positive hedonic value associated with courtship and mating—can act as a reinforcer in a variety of contexts. Indeed, animals can be trained to develop fetishes: strong, specific preferences for arbitrary stimuli. Pfaus et al. (2012) trained male rats to associate copulation with wearing a rodent jacket. After training, males were sexually aroused by being fitted with the jacket, and even showed reduced sexual activity when exposed unclothed to females. Çetinkaya and Domjan (2006) used a similar paradigm to train male quail to mount a "terrycloth object." Any stimulus thus has the potential to be associated with sexual reward, or, conversely, with negative sexual experiences, although the latter have received less attention. Associative learning can thus assign strong positive or negative hedonic value to arbitrary cues.

## Evaluative mechanisms and preference evolution

There are two important ways in which changes in evaluative mechanisms, independent of the sensory periphery, affect the evolution of preferences and their coevolution with signals. First, evaluative mechanisms provide a release from constraints imposed on sensory systems, and perhaps—as in songbirds, where it is performed in two distinct anatomical regions—a broader mutational target than the sensory periphery. Constraints may be imposed by ecological function, like the variety of visual tasks optimized by spectral tuning in a given light environment, or by basic structural constraints like release from habituation or retinal response to spatiotemporal contrast (Rosenthal 2007). The mechanisms described above suggest that indifference or avoidance of stimuli eliciting greater sensory response can evolve without compromising sensory function.

The second important way in which evaluative mechanisms influence preferences and signals is in their potential to induce abrupt changes in preferences. Changes in evaluation—how hedonic value is assigned to stimuli—may underlie much of preference evolution, and coevolution among traits, within the constraints imposed by sensory envelopes. Importantly, the mechanisms involved suggest that "flips" in hedonic value—reversals such that previously attractive stimuli rapidly become unattractive and vice versa—may be quite common.

Allowing for such "flips" in evolutionary models may shed light on processes like trait-preference evolution through sexual conflict, or the role of mate choice in speciation. Turner and Burrows' (1995) model of sympatric speciation showed that assortative mating could evolve readily within a population if a mutation acted to reverse chooser preference from one trait extreme to another. This assumption that preferences could thus evolve was criticized and largely discarded by subsequent models: most quantitative-genetic models of preference evolution assume that preferences evolve along a continuum: that is, allelic variation around a strong preference is associated with preferences that are slightly weaker, as opposed to absent or reversed. Relaxing this assumption, to account for the broad shifts permitted by changes in evaluation, could shed light on a number of lingering puzzles in sexual selection, like frequent losses of sexually-dimorphic traits (Wiens 2001), the evolution of multicomponent trait and preferences (Candolin 2003; van Doorn and Weissing 2004; Bro-Jørgensen 2010), and diversification of traits and preferences within and among populations (Bondurianksy 2011; Rodríguez et al. 2013).

In particular, a deeper consideration of evaluative mechanisms can help us more fully consider the role that mate choice can play in speciation and hybridization. Beyond sympatric speciation, abrupt shifts in preference may facilitate a range of processes involving trait divergence, from diversification through sexual conflict (Gavrilets 2000) to the maintenance of signal polymorphisms (Puebla et al. 2007).

Recent work has called attention to the evolutionary importance of hybridization and to the role of mating decisions in shaping the evolutionary origin and fate of hybrids. In particular, environmental effects can impact mate choice for conspecifics or heterospecifics, and hybridization can shape mate-choice mechanisms in ways that facilitate or inhibit reproductive isolation and gene flow within species. Hybridization can sometimes be attributed to environmental changes affecting the sensory periphery. A striking adaptive example of environmental cues acting on evaluative mechanisms, however, is found in spadefoot toads. Pfennig (2000, 2007) showed that under high-water conditions, females preferred the calls of conspecifics. Under drought conditions, they reversed their preferences, favoring faster-developing heterospecifics more likely to survive to the metamorphosis in shallow water.

Hybridization can also shape evaluative mechanisms in nonintuitive ways. A little-remembered paper in *Nature* by Tebb and Thoday (1956) was ahead of its time in controlling the social environment and systematically varying the thermal regime to test effects on mate choice. Females from both the *white* and *white-apricot* lines of *D. melanogaster* preferred *white-apricot* males over *white* males, but this preference was reversed in first-generation hybrid females. The preference reversal is in contrast to other systems where early-generation hybrids show intermediate or weakened preferences consistent with changes at the sensory periphery. Hybridization can thus generate novel preferences through its effect on evaluative mechanisms.

## Evaluation, learning, and evolution

The way in which experience shapes mate choice, or does not, is crucial to how sexual selection operates and to the evolutionary dynamics of assortative mating and speciation. As noted above, the effects of experience can take myriad forms, from sexual imprinting to predator-induced loss of preference. The phenotypic effect of experience varies across populations and species, suggesting genotype × environment interactions. A useful metric for studying this interaction is the coefficient of social interaction, $\psi$, which ranges from positive to negative across field crickets studied by Bailey and Zuk (2012). Similarly, both developmental (Verzijden and Rosenthal 2011; Cui et al. 2017) and short-term (Verzijden et al. 2012) experience has opposite effects on two hybridizing sister species of swordtails, *Xiphophorus birchmanni* and *X. malinche*. The social interaction coefficient $\psi$ is positive for *X. birchmanni*: exposure to heterospecific cues increases preference for heterospecifics, and exposure to conspecifics increases preferences for conspecifics. Female *X. malinche*, in contrast, develop antipathy for *X. birchmanni* cues. There is an "instinct to learn" (Marler 1991) that differs between these species: the same cues that are evaluated positively in *X. birchmanni* are evaluated negatively in *X. malinche*.

It is useful to consider variation in $\psi$ in terms how individuals' evaluative mechanisms process these experiences. For example, stimuli associated with positive experiences or cues will acquire positive hedonic value ($\eta > 0$) through associative learning, and vice versa for negative experiences. Neutrally evaluated cues ($\eta \sim 0$) will have little effect on subsequent behavior. The social interaction coefficient, $\psi$, ultimately emerges from how these interactions are evaluated, and should be expected to covary positively with $\eta$.

Considering the interdependence of $\psi$ and $\eta$ should shed light on variation in experiential effects in mate choice. In *Xiphophorus*, testable hypotheses include an *Ostrinia*-style switch in the outputs of odorant receptor neurons sensitive to *birchmanni*-specific cues, or baseline personality differences that lead to different labeling of the same social interactions (with shy *X. malinche* responding negatively to interactions with bold *X. birchmanni* males). Evaluation and hedonic value provide a framework for thinking about these mechanisms and how they could differ between species.

## Summary and Conclusions

There are few, if any, aphrodisiacs in nature. Evaluative mechanisms are an essential part of decision-making that connects sensory stimulation to behavioral decisions. Evaluation underlies much of the complexity in mate choice: how decisions are modulated by the social and environmental context, how preferences can evolve in the face of strong sensory constraints. Evaluation is also required for choosers to avoid more-salient stimuli, and provides one route for modulating whether or not they attend to particular signals. Theory predicts reduction or reversal of preferences under many conditions, notably arbitrary coevolution of traits and preferences and direct selection on preferences, including through sexual conflict (Holland and Rice 1998; Rosenthal and Servedio 1999; Wiens 2001; reviewed in Rosenthal 2017). The genetic and environmental forces shaping preferences can act powerfully through evaluative mechanisms even when the sensory periphery is conserved. This has important implications for preference evolution, for trait evolution, and for the dynamics of reproductive isolation and gene flow. Considering evaluation is also useful in understanding phenomena like sexual dimorphism in preferences (Kimura et al. 2005; Hoke et al. 2010) and stable sexual preference in humans (Kranz and Ishai 2006) This is because specific genetic or environmental changes can radically change preferences, even reversing them, through their effects on the neural mechanisms underlying evaluation.

The integration of neuroscience, ecology, and behavior under a sensory framework has produced unprecedented insights in our understanding of evolution, and recent work has fruitfully applied a similar approach to the challenge of understanding the role of cognitive and decision-making processes (Ryan and Cummings 2013; Ryan 2018). Sensation, perception, and evaluation are all integrated over the course of a mating decision, and are likely to be interrelated in ways beyond those discussed here. In particular, stimuli that are more perceptually salient are more likely to be learned and remembered than those that are not, so that "flips" between extreme positive or negative preferences might be more likely than shifts for less-preferred traits. Similarly, Reber et al. (2004) suggest that "beauty in the processing experience"—ease of perceptual processing—might provide an inherent hedonic reward.

A quarter-century of sensory perspectives on animal communication has fundamentally changed the way we think about behavioral evolution. Over the next 25 years, I suggest it is worth building theoretical and empirical research programs around the evolution and function of communication mechanisms beyond the sensory periphery, with the same intellectual rigor and breadth that has characterized sensory exploitation and sensory drive.

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