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Understanding the Role of Incentive Salience in Sexual Decision-Making

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Synopsis In the search for understanding female sexual decision-making, progress has been made in uncovering a variety of perceptual biases and most of these concern the animal’s sensory biology and cognitive processes. We are now poised to dig deeper into the female’s decision-making and ask if incentive salience, which plays a role in all types of appetitive behaviors, also influences a female’s “taste for the beautiful.” The incentive salience hypothesis suggests that dopamine assigns value or salience to objects or actions. After value is assigned to all potential actions, an action selection system then chooses among potential options to select the most valuable action. In this view, dopamine stimulates reward-seeking behavior by assigning incentive salience to specific behavioral actions, which in turn, increases pursuit and focus on objects or stimuli that represent the valuable action. Here, we apply this framework to understand why females are compelled to respond maximally to some male courtship signals over others and how this process may reveal a female’s hidden mate preferences. We examine studies of dopamine and the mesolimbic reward system because these may play a role in expanding the female’s perceptual landscape for novelty in male courtship signals and establishing novel hidden preferences. We review three avenues of research that may identify signatures of incentive salience in females during sexual decision-making. This review includes studies of dopamine agonist or antagonist administration in females during mate choice or partner preference tests, measures of neural activity in dopaminergic neural circuits during mate choice or partner preference tests, and social regulation of dopamine in females when entering reproductive contexts and/or exposure to mate signals. By applying the incentive salience hypothesis to female reproductive decision-making, it redefines how we see the female’s role in sexual encounters. Females cannot be considered passive during reproductive encounters; rather they are seeking sexual encounters, particularly with males that tap into their perceptual biases and initiate a reward-seeking response. Incentive salience applied to reproductive behavior requires considering females as viewing sexual stimuli as rewarding and initiating action to seek out this reward, all of which indicates females are driving sexual encounters.

Introduction

Sensory biases underlie an animals’ predisposition to respond to specific communication signals and these biases guide decision-making in various social contexts (Jennions and Petrie 1997; Endler and Basolo 1998; Ryan 1998; ten Cate and Rowe 2007). The definition of sensory biases, however, has recently expanded as it is now also well-established that various cognitive processes also influence an animals’ responses to signals. The collective sensory and

cognitive processes that shape an animals’ predisposition to respond to one signal over another form the perceptual biases of that animal (Ryan and Cummings 2013). It is important to consider that these perceptual biases are not fixed, but instead the sensory and cognitive processes that form perceptual biases are plastic, ever-changing processes. Dynamic regulation of the neural mechanisms associated with perceptual biases allows animals to match their behavioral responses to social or environmental

stimuli with their internal state. For example, an animal in an extreme state of hunger will process food-related sensory cues differently from an animal that is well-fed. The hungry animal will assign greater value or salience to these cues and respond vigorously, whereas the well-fed animal may not assign great value to the same cue and may therefore not respond at all (Pompilio et al. 2006; Hemingway et al. 2020). This is due, in part, to neuromodulation of sensory and cognitive mechanisms that act collectively to define the external stimuli that should be assigned meaning or incentive salience. This has been termed the incentive salience hypothesis and it has gained much attention in studies of drug seeking and addictive behavior (Berridge and Robinson 1998; Berridge 2007; Smith et al. 2011). But how can we apply it to understand sexual decision-making, particularly with respect to females?

The incentive salience hypothesis suggests that dopamine is needed to assign value or salience to objects or actions. Once values are assigned to all options for a potential behavioral response via the actions of dopamine, the values are then available for an action selection system that chooses the most valuable action (McClure et al. 2003). Thus, it is thought that dopamine does not simply mediate the hedonic effect of a reward but rather it stimulates reward-seeking behavior by assigning incentive salience to specific behavioral actions. Once incentive salience is assigned to a specific action, an animal should increase pursuit of an object that represents that action and work hard to obtain it. Berridge and Robinson (1998) describes dopamine as assigning incentive salience to a behavioral action by transforming the neural representation of the stimulus or action into an object of attraction that the animal will pursue with singular focus. Here, we apply the incentive salience hypothesis described by psychologists to our question of decision-making in sexual contexts. We apply this framework to understand female sexual decision-making and particularly to understand why females are compelled to respond maximally to some male signals over others and how this process may reveal a female's hidden mate preferences.

Applying incentive salience to sexual decision-making

Dopamine may act in three ways to influence behavior. It may act as a mechanism that stamps in associative relationships (i.e., learning); it may mediate hedonic aspects of an action (i.e., liking); it may motivate the pursuit of a reward, which leads to

reward-seeking behavior (i.e., wanting). The “wanting” category is the incentive salience category in which signals associated with reward are transformed into highly desirable, attractive targets that command attention and stimulate pursuit (Berridge and Robinson 1998; Ikemoto and Panksepp 1999; Berridge 2007; Salamone et al. 2005). It is important to consider that “wanting” does not come about without “learning and liking” but dopamine's role in “liking” sexual stimuli is less substantive when compared with the evidence supporting the hedonic effects of opioids during sexual encounters (Paredes 2014).

Distinguishing between each of the three possible dopaminergic roles is complex, but the timing of dopamine release relative to the reward-motivated action is key to identifying which role dopamine is playing. Ikemoto and Panksepp (1999) describes incentive salience as a dopaminergic regulation of appetitive behaviors but not consummatory behaviors (Ikemoto and Panksepp 1999). For example, increased dopaminergic activity immediately prior to reward-motivated behavior, not during, indicates that dopamine's role is to stimulate reward-seeking behavior rather than mediating hedonic aspects of that behavior. Studies in rodents demonstrate that increased dopaminergic activity occurs just prior to reward-motivated action (Montague et al. 1996; Schultz 1998). Moreover, dopamine antagonism does not alter affective reactions to rewards, indicating hedonic responses to a reward-motivated action remain intact (Ikemoto and Panksepp 1999). Studies of dopamine receptor antagonism indicate dopamine does not alter hedonic aspects of a reward but instead inhibits the initiation of any action needed to obtain the reward (Salamone et al. 1997; Berridge and Robinson 1998; Ikemoto and Panksepp 1999; Salamone and Correa 2002). These studies suggest that internal valuation of a reward remains unaltered by this blockade, but the capacity to act on that valuation is altered as the animals' capacity to act becomes inhibited (Ikemoto and Panksepp 1999). Thus, dopamine release should occur in anticipation of desirable rewards and initiates vigorous reward-seeking behavior when the stimulus is presented.

An additional key point in understanding dopamine's role in mediating reward-motivated actions is that the animal must be in a heightened state of motivation. For instance, in the example used above, odors associated with food rewards may be “liked” by an animal but will not be transformed into “want” until the animal is hungry (Berridge 2007). This further suggests that the timing of dopamine is key to transforming an animal's behavioral response.

Dopamine activity must occur during a heightened state of sexual motivation for the animal to assign incentive salience to an object or action, and then to respond as if it is a highly desirable, attractive target that is commanding attention and stimulating pursuit.

Here, we examine the possibility that incentive salience plays a role in sexual decision-making, particularly in females that are assessing potential mates. In females, heightened sexual motivation is achieved mostly via the actions of estrogens. Elevated circulating estrogen enhances motivation to mate, which sets the stage for dopamine to act within mesolimbic reward centers (and other areas with social decision-making brain regions; O'Connell and Hofmann 2011) to assign salience to specific male courtship signals. Against a physiological background of elevated estrogens, dopamine surges may act on specific neural targets to stimulate the female's pursuit of incentive signals. These neural targets are the same targets that collectively define the females' perceptual biases as they belong to sensory and cognitive processes. Moreover, there is functional overlap between estrogen and dopamine during reproduction (Pasqualini et al. 1995; Kabelik et al. 2011) and significant overlap in the neural targets of these neuromodulators as estrogen receptors reside on dopaminergic cells within the mesolimbic reward system, which sets up cross-talk between these neuromodulators (Maney et al. 2001; LeBlanc et al. 2007). Thus, it is possible that as elevated estradiol heightens a females' interest in sex, dopamine is released in neural reward centers to facilitate defining signals with incentive versus signals without incentive. Simultaneously, both neuromodulators may target sensory regions and modify how the female hears, sees, or smells sexual signals thereby increasing the likelihood she will detect the signal when it is present and possibly enhance her ability to notice differences between signals.

Looking for evidence of incentive salience in reproductive decisions

We examine three avenues of research to understand the action of dopamine in female mate choice and to search for signatures of incentive salience in females during sexual decisions. Avenues of research that may reveal potential for incentive salience during sexual decision-making include studies of (1) dopamine agonist or antagonist administration in females during mate choice or partner preference tests; (2) measures of neural activity in dopaminergic neural circuits during mate choice or partner preference

tests; and (3) social regulation of dopamine in females when entering reproductive contexts and/or exposure to mate signals. Together, these studies may identify signatures of incentive salience in females during their decision-making process in mating contexts.

The reward system in the brain and the specific actions of dopamine within the reward system have been demonstrated to be involved in both consummatory and appetitive aspects of reproduction and reproductive decision-making in a variety of female vertebrates (Meisel et al. 1993; Mermelstein and Becker 1995; Pfau et al. 1995; Becker et al. 2001; Aragona et al. 2003; Fisher et al. 2005; Pawlisch and Ritters 2010; Alger et al. 2011; Forlano et al. 2017). While many of these studies do not explore the combined roles of estradiol and dopamine on female reproductive decision-making, it is the case that these tests are done in reproductively active females that are already showing some interest in male signals. Thus, presumably these female subjects already possess the necessary elevated estrogen levels prior to starting these experiments. For instance, in reproductive female European starlings (*Sternus vulgaris*), stimulation of dopamine receptors using peripheral injections of a non-selective dopamine reuptake inhibitor (GBR-12909; an indirect dopamine receptor agonist) initiated female responses to a song stimulus that would normally not be attractive. In this case, dopamine eliminated selective female responses to male song so much so that it induced female responses to heterospecific songs (Pawlisch and Ritters 2010). These results suggest that dopamine transforms a previously unattractive stimulus into one that initiates approach from the female. In addition, in a preliminary study of female túngara frogs (*Physalaemus [=Engystomops] pustulosus*), dopamine might also play a role in mate choice decisions. In this case, a non-selective dopamine agonist (apomorphine) was administered to reproductively active females just prior to exposure to a synthetic non-conspecific mating call known to be unattractive from a previous study (Ryan et al. 2003; Ryan et al., unpublished data). Treated females now found these calls attractive. While it is unclear whether dopamine stimulates response to these mate signals via a "learning, liking, or wanting" mechanism, these studies suggest that dopamine might play a role in expanding the females' "preference landscape."

It is important to note, however, that there are two families of dopamine receptors: D1-like, which includes D1 and D5 receptors, and D2-like, which includes D2, D3, and D4 receptors (Neve et al. 2004). Apomorphine binds D1-like receptors but it

binds D2-like receptors with a much greater affinity (Missale et al. 1998). Thus, studies are needed to isolate which receptor type mediates changes in selectivity and whether dopamine is modifying mate preference via “learning or wanting” mechanisms. For instance, D2-like receptors are thought to be involved in salience assignment or “wanting” during partner preference tests in prairie voles. In studies of reproductive female prairie voles, blockage of dopamine receptors with non-selective antagonist (haloperidol) abolishes mating-induced partner preference formation. Low dose infusion of a non-selective dopamine agonist (apomorphine) induces significant partner preference for familiar mates, whereas high dose infusions of apomorphine do not (Aragona et al. 2003). Further testing of the effects of receptor-specific dopaminergic drugs revealed that brain region-specific activation of D2-like receptors induced partner preferences in the absence of mating, whereas brain region-specific activation of D1-like receptors failed to induce partner preferences. Moreover, when a cocktail of D1 and D2 agonists were co-infused, the addition of the D1 agonist altered previous results by preventing partner preferences that were induced by D2-like activation (Aragona et al. 2003). Thus, it is important to distinguish between the various receptor types to identify the mechanism by which dopamine acts to stimulate pursuit of objects, actions, or stimuli that have been previously assigned value and therefore, incentive salience.

Studies examining differential brain region responses during mate choice can also provide insight into the role of dopamine in sexual decision-making and possibly incentive salience. Examining levels of neural activity within dopaminergic circuitry or other measures of dopamine action such as dopamine synthesis, release, or quantifying dopamine metabolites have been applied to various studies of mate choice/preference in nearly every major vertebrate group, including humans (Meisel et al. 1993; Mermelstein and Becker 1995; Pfaus et al. 1995; Becker et al. 2001; Aragona et al. 2003; Fisher et al. 2005; Kranz and Ishai 2006; Sockman and Salvante 2008; Chakraborty et al. 2010; Hoke et al. 2010; Alger et al. 2011; Matragrano et al. 2012; Maney 2013; Forlano et al. 2017). For example, in humans, presentation of a picture of one’s partner increases activation of dopaminergic circuitry (Fisher et al. 2005). Also, in a related study, homosexual and heterosexual men and women rated the attractiveness of faces and fMRI showed similar amounts of activation in areas of the brain involved in face recognition among the four groups. But when reward

areas of the brain were measured, there was variation among subjects and sexual orientation; heterosexual women and homosexual men both showed enhanced activation of the reward circuit when they viewed men’s faces, while homosexual women and heterosexual men showed enhanced activation of the same circuit when they viewed women’s faces (Kranz and Ishai 2006). These results indicate the reward system exhibits mate preference-based rather than gender-based responses.

There are numerous brain regions involved in decision-making across various social contexts, including sexual decision-making (O’Connell and Hofmann 2011). Some studies explore these regions via functional connectivity maps. For example, activity-dependent immediate early gene (IEG) expression in female plainfin midshipman fish (*Porichthys notatus*) identified neural networks associated with responsiveness to acoustic cues during mate localization. Comparison of functional connectivity maps in unmotivated and motivated females revealed an important role for dopaminergic neurons in various hypothalamic regions, including the pre-optic area, the ventral thalamus, and the dorsomedial telencephalon, a region homologous to the laterobasal amygdala (Forlano et al. 2017). Other IEG studies show that female white-throated sparrows (*Zonotrichia albicollis*) and túngara frogs exhibit a correlation between neural activity in the mesolimbic reward system after exposure to conspecific mate signals (Chakraborty et al. 2010; Hoke et al. 2010; Maney 2013). Finally, in female prairie voles, pharmacological activation of dopamine receptors within the nucleus accumbens (NAc) is sufficient to facilitate female choice of familiar partners. More specifically, activation of D2-like receptors within the NAc shell, but not the NAc core, induced partner preferences in female prairie voles (Aragona et al. 2003; Aragona and Wang 2009). Together, these studies describe a clear role for dopaminergic and reward circuitry in sexual decision-making even though it is not yet clear if dopamine is facilitating these behaviors through a “learning, liking, or wanting” mechanism. Moreover, it would be interesting to determine whether dopamine’s mechanism of action during sexual decision-making is conserved across these different taxonomic examples or whether dopamine plays a unique role in partner preference formation and/or mate choice decision-making across vertebrates.

The final avenue to search for signatures of incentive salience in females during sexual decision-making is to ask whether dopamine is regulated by exposure to sexual stimuli, particularly within the

sensory and cognitive brain regions that form the females' perceptual biases. That is, can dopaminergic reward circuitry be socially regulated by male mate signals in females within sexual contexts? These studies may be particularly interesting to understand the role of incentive salience in sexual decision-making because in these cases, dopamine is released in response to the signal rather than during consummation of sexual behavior. Thus, dopamine activity occurs during an anticipatory phase or an appetitive phase and may therefore initiate reward-seeking, which in this case would be a sexual encounter. For example, receiving courtship displays likely induces dopamine synthesis in reward circuitry, specifically the VTA in female zebra finches, which exhibit dense tyrosine hydroxylase immunoreactivity (TH-ir) in NAc when housed with a male compared with a female (Alger et al. 2011). There is also a positive correlation between TH-ir in the ventral medial hypothalamus (VMH) and the ventral tegmental area (VTA) and the amount of courtship a female received from her partner (Alger et al. 2011). While elevated TH-ir within reward circuitry does not respond with increased IEG expression to simple playback of songs (Svec et al. 2009; Lynch et al. 2012) other regions containing TH do respond during simple song playback experiments, particularly the locus coeruleus; a region that is predominately noradrenergic in nature (Lynch et al. 2012). However, electrophysiological studies of neural responses in mesolimbic reward centers of females or *in vivo* microdialysis of these regions in songbirds during song exposure may provide more insight as IEG protein expression in areas such as NAc and VTA is not especially robust (Lynch et al. 2012). In rodents, paced-mating (i.e., female control of the timing of male mounts, intromission, and ejaculation) is associated with higher dopamine in reward-related brain regions compared with non-paced mating (Mermelstein and Becker 1995; Becker et al. 2001). However, two of these studies also demonstrate that the release of dopamine in striatal or mesolimbic regions occurs in anticipation of sexual encounters (Meisel et al. 1993; Pfau et al. 1995). Using *in vivo* microdialysis, it was reported that a rapid surge in ventral striatal dopamine in females shortly after exposure to the male, which gradually declined over the next 45 min but remained significantly above baseline while exposure to the male continued (Meisel et al. 1993). Likewise, in another microdialysis study, it was also reported that dopamine significantly increased in females within the NAc after exposure to sexually active males that they could see and smell but could not interact with (Pfau

et al. 1995). The timing in which the initial dopamine surge occurs in these studies provides compelling evidence that dopamine is involved in appetitive aspects of sexual behavior and may be released upon encounter with stimuli that have been assigned incentive salience. Moreover, these studies suggest that female responses to male sexual signals may be considered a reward-motivated response, indicating that incentive salience and other processes that influence other appetitive behaviors such as food- and drug-seeking may also be applied to female sexual decision-making.

There is converging evidence for incentive salience in female sexual decision-making from studies of dopamine and dopamine receptor manipulation, neural activity in dopaminergic circuits, dopamine release and metabolism, and dopamine-containing cellular responses to sexual or courtship stimuli. These studies indicate that dopamine targets both the sensory and cognitive brain regions comprising the females' perceptual biases. The actions of both dopamine and opioids (Ventura-Aquino et al. 2018) within brain regions that encode perceptual biases in sexual contexts may facilitate how females define which courtship signals are meaningful and initiate pursuit of the meaningful signals.

Connecting incentive motivation and incentive salience in female sexual behavior

There has been much work done on the role of dopamine in incentive motivation in female rodents, albeit not as much as has been done in males. Studies that focus on dopamine's role in female sexual behavior in rodents produce contradictory results with no easy interpretation regarding the effects of dopamine on female sexual behavior. These studies are confounded by the fact that the same type of dopamine treatment administered at the same dose can have strikingly different effects on female sexual behavior depending on the hormonal environment of the female (Ågmo 1999). In addition, dopamine treatments affect motor activity, which makes it difficult to distinguish between true dopamine-dependent modifications in motivation versus changes in ambulatory behavior or other motor patterns. However, some key points do emerge from these collective studies. First, as mentioned above, incentive salience is steeped within sexual motivation and appears to be an emergent property of motivation. Second, while there are no systematic studies that distinguish between the effects of dopamine in mediating "learning, liking, and wanting" with

respect to female sexual behavior, results demonstrate that dopamine has strikingly different effects on sexual motivation in female rodents depending on the hormonal environment. As hormone-dependent sexual motivation changes, so does the influence of dopamine on incentive salience. The connection between incentive motivation and incentive salience has been drawn by [Ventura-Aquino et al. \(2018\)](#) in which these authors describe the roles of dopamine in stimulating “wanting” and opioids in stimulating “liking.” Here, we discuss the importance of considering studies of sexual decision-making in the light of the incentive salience hypothesis to understand how the brain transforms “learned or liked” sexual signals into signals that are “wanted.”

To begin this discussion, it is useful to divide female sexual behavior into two components: (1) detection, approach, and contact of suitable mates and (2) copulation or everything that happens after contact is made in the case of animals in which no intromission occurs. This discussion focuses solely on the former category as these behaviors are contained within the sexual decision-making stage. The role of dopamine in regulating approach/contact (i.e., appetitive) behaviors in females can be considered as falling into “learning, liking, or wanting.” For example, those studies that examine dopamine’s role in facilitating sexually experienced versus inexperienced female responses to males or male courtship stimuli would fall into the “learning or liking” category ([Kohlert and Meisel 1999](#)). Those studies that focus on the role of dopamine in reinforcing or rewarding sexual behavior in sexually experienced and inexperienced females can also be considered as focusing on “learning or liking” sexual stimuli. Many of these studies utilize condition place preference paradigms or compare female paced mating with non-paced mating ([Paredes and Alonso 1997](#); [Paredes and Vázquez 1999](#); [Martinez and Paredes 2001](#); [Guarraci and Clark 2003](#); [Ellingsen and Ågmo 2004](#)). Finally, studies that explicitly control the female’s sexual motivation via manipulation of her hormonal environment prior to dopamine treatment are tapping into the last category; “wanting.” “Wanting” is described by [Berridge and Robinson \(1998\)](#) as only occurring during heightened motivational state. For example, as discussed above, foods that we “like” are not “wanted” unless we feel hunger. An analogous phenomenon is observed in appetitive sexual behavior as females that have recently mated spend less time near sexual incentives, indicating a lack of motivation or interest in mating-related stimuli ([Ågmo et al. 2004](#)) likely as a consequence of sexual satiety. Studies that attempt to first

heighten the female’s sexual motivation via hormones before studying the effects of dopamine fall into the category of understanding incentive salience as it is applied to other appetitive behaviors such as food or drug seeking. Moreover, studies that focus on dopamine surges or administration just prior to the female’s approach/contact of suitable mates are identifying if dopamine plays a role in stimulating pursuit of a rewarding stimulus while in a heightened sexually motivated state. Each of these various types of studies have been performed and each tell us something different about how dopamine regulates the different components contained within the incentive salience hypothesis (learn, like, and want). The purpose of this discussion is not to provide an exhaustive review of the manner in which dopamine modifies female sexual behavior as there are excellent reviews already on this subject ([Ågmo 1999](#); [Paredes and Ågmo 2004](#)). Instead, the purpose of this discussion is to point out the parallels between the two bodies of literature (i.e., incentive motivation and incentive salience) and to suggest that systematic investigations into how the brain transforms “learned or liked” sexual signals into “want” via the actions of dopamine against a backdrop of a controlled internal (i.e., hormone) environment are needed.

How incentive salience may reveal hidden mate preferences

In many animal species in the wild, males advertise their sexual wares to females, who in turn choose the male they find most attractive. In some cases, males advertise their prowess as parents or the abundance of resources they control yet in other cases, female mate choice is motivated by the females’ aesthetics, her “taste for the beautiful” ([Darwin 1871](#); [Ryan 2018](#)), rather than their utilitarian needs. It is the females’ perceptual biases that define her attraction to a specific athletic display, a spectacular color, or a complex odor or sound. As described by [Darwin \(1871\)](#), these biases appeal to the females’ sexual aesthetic ([Richards 2017](#)). These perceptual biases can exist for many reasons. For example, fish have heightened sensitivity to colors of their main food items, which in turn, causes males to evolve those same colors into their sexual displays ([Rodd et al. 2002](#); [Garcia and Ramirez 2005](#); [Cummings 2007](#)). Frogs have two separate hearing organs for communication and in some species the male’s courtship call will stimulate only one of those hearing organs, but if males evolve an acoustic component that stimulates the additional hearing organ, the call becomes

more attractive to females (Ryan et al. 1990; Wilczynski et al. 2001). When sexual traits evolve in this manner, it indicates males have evolved traits that exploit hidden preferences in the females (Ryan and Cummings 2013). These preferences are not expressed prior to the evolution of the attractive trait and only appear when a male trait evolves to trigger the expression of the female's hidden preference. This idea is similar to Darwin's notion that female animals have inherent aesthetic preferences and that over evolutionary time males evolve traits that best match these preferences (Darwin 1871). This idea has received substantial traction recently in both the scientific and the general science literature (Rosenthal 2017; Ryan 2018) but it is still mostly not well understood how the females' perceptual biases contribute to hidden preferences and how it can be modulated in such a manner as to uncover preferences for traits she doesn't experience on a day-to-day basis.

As noted above, the dopamine reward system has been implicated in mating decisions in a variety of animals. For the most part these studies investigate decisions made by females about extant male courtship signals. But might dopamine also play a role in hidden female preferences? We do know in humans, and model organisms used to infer human biology, that this reward system has been implicated in the use of drugs (Volkow et al. 2011), pornography (Hilton 2013), overeating (Stice et al. 2010), gambling (Comings et al. 1996), and even general novelty seeking behavior in non-human primates (i.e., monkeys; Costa et al. 2014). It should be noted that because the reward system is involved in behavior that might be addictive it does not by itself indicate that the reward system is the cause of addiction (e.g., see Nutt et al. 2015). In most of these examples, the reward system can be thought of as expanding the landscape of human preferences for stimuli, either in quality or in quantity, that might not have been common in our distant evolutionary past. Might dopamine play a similar role in expanding the female's perceptual landscape for novel stimuli in male courtship signals? Might the reward system play a role in establishing novel hidden preferences?

Incentive salience redefines how we view the female's perspective during reproduction

Darwin's view of sexual selection and female mate choice (1871) put females in the driver seat as it was their "taste for the beautiful" that drove males in many species to evolve traits that were maladaptive

for survivorship. This emphasis on the female's evolutionary power cost him substantial support among his colleagues in Victorian England such as Alfred Wallace (Richards 2017; Ryan Forthcoming 2020). But when discussion of human mating systems arose, Darwin reverted to the common Victorian mores and assigned women much less of a role in decision-making. Even when female mate choice was promoted by Trivers (1972) and generally accepted throughout the field of sexual selection, there still managed to be a male-centric aspect of this line of work. Much of the research assumed that males possess traits that indicate their genetic quality and it is incumbent on females to evolve preferences for these superior male traits (Hamilton and Zuk 1982; Zahavi and Zahavi 1997). But in the last couple of decades there has been an enhanced emphasis on females and their perceptual and cognitive biases which may arise in the context of mate choice as well as other domains that might ultimately affect mate choice. When this is the case, it is the males that are scrambling, in an evolutionary sense, to evolve traits that will match the female's biases, such that the trait will complement her taste for the beautiful (Rosenthal 2017; Ryan 2018).

In the search for an understanding of a female's "taste for the beautiful," progress has been made in uncovering various perceptual biases and most of these concern the animal's sensory biology and cognitive processes. We are now poised to dig deeper into the female's decision-making and ask if incentive salience does indeed play a role in all types of appetitive behaviors, including sex-, food-, and drug-seeking. This redefines how we see the female's role in sexual encounters. Females are not passive during reproductive encounters; rather they are seeking out sexual encounters, particularly with males that tap into their perceptual biases and initiate a reward-seeking response. This implies females should be proceptive actors in all sexual encounters rather than receptive to male stimuli. In short, incentive salience applied to reproductive behavior requires that we consider females as viewing sexual stimuli as rewarding and initiating action to seek out this reward, all of which indicates females are driving sexual encounters.

Future directions; applying incentive salience to non-model systems to understand hidden female preferences

Systematic investigations into "learning, liking, and wanting" are needed in both animals that are model systems and non-model animal systems studied

under natural or semi-natural conditions (for review see Ventura-Aquino et al. 2018). Moreover, by pairing studies of incentive salience to studies of non-model systems with a long history of information on female preference functions (i.e., preference for signals along a continuum of stepwise changes in the signal) can provide critical insight into how female preferences for signals evolve. For instance, if dopamine release stimulates female approach behavior to a male courtship signal and opioid release reinforces her “liking” of the signal once mating has occurred, it is possible that in subsequent mating events, dopamine release will mark the courtship signal that has incentive (i.e., associated with reward in the past) and any signal with similar characteristics. This increases the probability that the female will repeat the same response to signals she has encountered already along with a continuum of signals that contain similar characteristics. This has profound implications in understanding the evolution of communication signals. Thus, understanding how the brain defines what is a meaningful signal that contains value or salience in a sexual context can provide critical insight into female receiver psychology and ultimately the evolution of animal signals.

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