Published in final edited form as:

Neurosci Biobehav Rev. 2011 October ; 35(9): 1837–1845. doi:10.1016/j.neubiorev.2010.12.017.

Pleasure seeking and birdsong

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Abstract

Songbirds sing at high rates within multiple contexts, suggesting that they are highly motivated to communicate and that the act of singing itself may be rewarding. Little is known about the neural regulation of the *motivation* to communicate. Dopamine and opioid neuropeptides play a primary role in reward seeking and sensory pleasure. In songbirds, these neurochemicals are found within brain regions implicated in both motivation and reward, including the medial preoptic nucleus (mPOA) and ventral tegmental area (VTA). Several lines of research indicate that dopamine and opioids in these regions play a role in birdsong that differs depending upon whether song is used to attract females (female-directed song) or is not directed towards other individuals (undirected song). Evidence is reviewed supporting the hypotheses 1) that distinct patterns of dopamine activity influence the motivation to produce undirected and female-directed song, 2) that undirected communication is intrinsically reinforced by immediate release of opioids induced by the act of singing, and 3) that directed communication is socially reinforced by opioids released as part of social interactions.

Keywords

communication; dopamine; opioids; medial preoptic nucleus; ventral tegmental area; song control system; reward; motivation; birdsong; social behavior; context

Vocal communication plays a crucial role in social interactions in many vertebrate species, including songbirds. Songbirds sing at high rates within multiple social contexts, suggesting that they are highly motivated to sing and that the act of song production itself may be rewarding. Much research has focused on the neural control of specific aspects of song such as learning and sensorimotor processing (for reviews see (Zeigler and Marler, 2004)). In contrast, little is known about the role of motivation and reward neural systems in the regulation of vocal communication within distinct social contexts. This review focuses on studies which together support the idea that dopamine underlies the motivation or drive to sing, that opioid release makes song production rewarding, and that the participation of opioid and dopamine systems in song differs depending upon the social context in which song is produced. As part of this special journal issue devoted to the career of Dr. Jaak Panksepp, I emphasize that many of his theories of affective neuroscience, pleasure, and motivation form the conceptual background for this review (e.g., (Burgdorf and Panksepp, 2006; Panksepp, 1998; Panksepp, 2005; Panksepp et al., 1978a; Panksepp and Moskal,

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2008; Panksepp et al., 1979; Panksepp et al., 2004; Panksepp et al., 1978b)). Alone, the fact that this review is focused on whether or not birds experience pleasure when singing is a tribute to the influence of Dr. Panksepp and his advancement of the field of Affective Neuroscience, which has opened the way for the study of animal emotions.

The factors reinforcing song production differ depending on the function of song

In songbirds, as in other species, a primary function of vocal behavior is to influence the behavior of other conspecifics. For example, male songbirds with elevated testosterone sing at high rates to attract females or to repel male competitors (Catchpole and Slater, 2008). Song produced in response to another individual or that serves to influence the behavior of another individual in songbirds is often referred to as **directed song** (Jarvis et al., 1998; Zann, 1996). Once directed song successfully influences a conspecific, in many cases this is accompanied by a temporary reduction in song production. For example males of many species, including our primary study species European starlings, sing less after attracting and pairing with a mate but increase song activity upon mate removal (e.g., (Cuthill and Hindmarsh, 1985; Krebs et al., 1981; Kroodsma et al., 1989; Logan and Hyatt, 1991; Otter and Ratcliffe, 1993)) or immediately prior to copulation (Eens and Pinxten, 1990; Eens and Pinxten, 1995; Pinxten and Eens, 1997). This suggests that the acquisition of a desired reward results in satiety and a temporary reduction in a male's motivation to sing. Because directed song can be immediately reinforced through attracting or repelling a conspecific, song in this context may be rewarded to a large extent through neurochemicals released in response to female proximity, during copulation or in response to threat reduction (i.e., when song successfully repels an intruder). Thus, directed song can be considered **socially reinforced** by the behavioral response of a conspecific. To illustrate the mechanisms by which motivation and reward neural systems shape vocal communication, in this review I will focus on directed song produced in response to a female (female-directed song), which can be considered highly sexually motivated and can be powerfully reinforced through copulation.

In addition to directed communication, songbirds as well as other vertebrates, produce vocalizations that are not directed towards and do not have any obvious, immediate effect on conspecifics. These vocalizations are common in large social flocks, do not attract females or repel males and appear to be ignored by potential recipients. In songbirds this form of communication is referred to as **undirected song** (Dunn and Zann, 1996; Jarvis et al., 1998; Zann, 1996). Undirected song is necessary for song learning and maintenance and may serve to maintain social flocks in adulthood. Undirected song does not result in any obvious, immediate social reinforcement (i.e., it does not immediately attract a female or repel a male). I propose that this form of song may be **intrinsically reinforced**; that is the *act of producing* undirected song, (rather than its consequences on conspecific behavior) may induce a rewarding neural state.

Dopamine, opioids, and the motivation to sing

Motivation (or anticipatory seeking behavior) and reward (or pleasure) are closely related, yet distinct components of behavior that rely on distinct neurochemical modulators (general concepts reviewed in (Panksepp, 1998; Panksepp and Moskal, 2008)). If a behavior results in reward (e.g., if directed song attracts a female or undirected song results in an intrinsic reward), this behavior is more likely to be repeated. If the reward is great, the animal will vigorously pursue the reward even in the face of obstacles (e.g., predators), reflecting a high degree of motivation. The neurotransmitter dopamine acting within mesolimbic and incertohypothalamic neural systems is well known for its role in motivation and reward;

however the precise role of dopamine in reward-related processes is contentious (see (Berridge, 2007; Panksepp and Moskal, 2008; Schultz, 2010; Wise, 2005)). Originally, it was proposed that dopamine release resulted in hedonic pleasure; however a growing body of research now supports the idea that rather than underlying reward itself, dopamine underlies reward seeking or the anticipation of reward (Berridge, 2007; Panksepp and Moskal, 2008). Panksepp proposes a unifying theory of dopamine function which posits that the role of dopamine is to energize a general neural system underlying anticipatory, reward seeking and expectancy necessary for an animal to eagerly engage in diverse activities, such as sexual behavior, social behavior, feeding, and foraging (Panksepp and Moskal, 2008). Here, this idea is extended to directed singing behavior. In contrast to reward seeking, the sensation of pleasure is not regulated by dopamine. Rather, other neurochemical systems, including opioid systems, act within mesolimbic and incertohypothalamic systems to underlie pleasure or reward (Agmo and Berenfeld, 1990; Burgdorf and Panksepp, 2006; Kelley et al., 2002; Pecina et al., 2006).

Given that female-directed song is highly sexually motivated, it is likely that dopaminergic systems which activate sexual motivation and reward seeking are strongly involved in song in this context. Once a male successfully attracts a female, I propose that physical interactions with the female or copulation result in a surge of opioid release within neural reward systems resulting in reward, followed by satiety and a temporary suppression of sexually-motivated song. Thus dopamine would be expected to **trigger and maintain** song; whereas, opioids would be expected to temporarily **inhibit** female-directed song.

Given that undirected song is not a sexually motivated behavior, dopamine in neural circuits involved in sexual motivation would not be expected to play a predominant role in this type of song; however, a male must be motivated in order to sing in any context, thus a pulse of dopamine may be associated with the initiation of undirected song. Given the expectation that the *act of producing* undirected song itself is rewarding, I predict that opioid release immediately induced by the act of singing serves to reinforce and maintain song production. Thus in the case of undirected song dopamine would be expected to **trigger** song; whereas, opioids would be expected to continuously **stimulate /maintain** undirected song.

Pharmacology studies demonstrate a stimulatory role for dopamine in female-directed song

Consistent with the prediction that dopamine is critical for sexually-motivated female-directed song, peripherally administered dopamine agonists stimulate whereas antagonists inhibit female-directed song (zebra finches (Rauceo et al., 2008); European starlings (Schroeder and Riters, 2006); Figure 1). The effects of peripheral manipulations of dopamine receptors on undirected song have not been well studied; however, a few studies indicate a role for dopamine in undirected vocal behavior. For example, a dopamine agonist increased general vocal behaviors in domestic chicks (de Lanerolle and Youngren, 1978). Furthermore in male zebra finches immediate early gene expression occurs in dopamine receptor containing neurons during both undirected and directed song in at least one brain region (area X; discussed in more detail below (Kubikova et al., 2010)), and dopamine in this region rises just prior to initiation of both female-directed and undirected song (Sasaki et al., 2006). However, in both of these studies relative differences were observed between birds singing directed and undirected song. Although the role of dopamine in undirected vocal production in other vertebrates has not been examined, the few studies examining directed communication suggest a well conserved role for dopamine. For example, in rats dopamine receptor agonists stimulate vocalizations associated with the anticipation of reward (50 kHz vocalizations (Wintink and Brudzynski, 2001)); whereas, antagonists

suppress sexually-motivated 50 kHz vocalizations produced by male rats in response to estrus females (Ciucci et al., 2009; Ciucci et al., 2007).

Opioids differentially influence female-directed and undirected song

Consistent with the prediction that opioid release leads to satiety and an inhibition of reward seeking, in male European starlings administration of an opioid receptor agonist strongly suppressed female-directed song ((Schroeder and Riters, 2006); Figure 1). Furthermore, treating males with an opioid receptor antagonist significantly increased female-directed song, an effect that was of low magnitude but observed in a majority of birds tested ((Riters et al., 2005); Figure 1). (For contradictory results see (Khurshid et al., 2010), in which a low dose but not two additional higher doses of opioid antagonist reduced directed song in male zebra finches). The findings in starlings are consistent with the results of multiple studies showing that opioid agonists generally inhibit whereas antagonists stimulate socio-sexual interactions (Carden et al., 1996; Herman and Panksepp, 1978; Kalin et al., 1995; Maney and Wingfield, 1998; Nocjar and Panksepp, 2007; Panksepp et al., 1980; Panksepp et al., 1978a; Panksepp et al., 1979; Plonsky and Freeman, 1982). If opioids underlie reward associated with song, then why would blocking opioids *increase* song production? One interpretation of these findings is that when opioids are low males actively seek sexual contact (reflected in female-directed song production) in order to attract a female to obtain opioid release and reward. Opioids released during social or sexual interactions then result in reward and satiety reflected in a temporary inhibition of social seeking (reflected in a reduction of female-directed singing). Studies across vertebrates suggest a well conserved role for opioids in directed communication. For example, opioid receptor blockade increased vocal behaviors produced in anticipation of social reward in socially experienced rats (Burgdorf and Panksepp, 2001) and vocalizations important for maintaining social contact in chicks and rat pups (Carden et al., 1996; Winslow and Insel, 1991). Furthermore, stimulation of mu or delta opioid receptors reduced social contact vocalizations in rat pups (Carden et al., 1991; Carden et al., 1996; Winslow and Insel, 1991).

Although few studies have examined opioid involvement in undirected song, data from a study in male zebra finches indicate that undirected song is inhibited by opioid antagonist injections (Khurshid et al., 2010). These findings are consistent with the prediction that opioids play a stimulatory role in song that is presumed to be intrinsically rewarding. This finding is similar to studies demonstrating that opioids stimulate the consumption of highly palatable food (i.e., feeding that can be considered intrinsically rewarding; e.g., (Glass et al., 1999; Gosnell et al., 1986; Morley, 1987)).

Sites of dopamine and opioid action

The incertohypothalamic and mesencephalic systems in which dopamine and opioids act are highly conserved across vertebrates and functionally similar in birds and mammals (Bharati and Goodson, 2006; Durstewitz et al., 1999; Goodson, 2005; Smeets and Gonzalez, 2000)). In songbirds, dopamine and opioids and their receptors or synthetic enzymes also richly innervate components of the song control system (Bottjer, 1993; Bottjer and Alexander, 1995; Deviche et al., 1993; Gullledge and DeViche, 1995; Heimovics and Riters, 2008; Kubikova et al., 2010), which is a specialized group of interconnected brain regions that is devoted to song learning, production, and sensorimotor processing (multiple reviews in (Ziegler and Marler, 2008)). Several song control regions display differential activity during directed and undirected song (Heimovics and Riters, 2005; Hessler and Doupe, 1999; Jarvis et al., 1998); however, there is no evidence that these regions participate in motivational aspects of song production (Bottjer et al., 1984; Nordeen and Nordeen, 1993; Nottebohm et al., 1976; Sohrabji et al., 1990). For example, lesions to song control region HVC (acronym

used as a proper name) abolish audible song production; however, birds with HVC lesions continue to assume a singing posture and display motor behaviors characteristic of song production (Nottebohm et al., 1976), suggesting an intact motivation to sing. Thus, it is likely that dopamine and opioids act within the song system to regulate song structure or sensorimotor processing but that these neurochemicals act outside of the song control system to regulate the motivation to sing.

For the purposes of this review I will focus primarily on the ventral tegmental area (VTA) and medial preoptic nucleus (mPOA), regions outside of the song control system for which a strong case can be made for differential dopamine and opioid regulation of directed and undirected song. Both of these regions are rich in dopamine and opioid receptors, proteins or synthetic enzymes (Heimovics et al., 2009; Heimovics and Riters, 2008; Kubikova et al., 2010; Riters et al., 2005; Woods et al., 2010). A role for dopamine in the mPOA in male sexual motivation is well established in rodents and in Japanese quail, a non-songbird avian species (Hull et al., 1995; Kleitz-Nelson et al., 2010a; Kleitz-Nelson et al., 2010b; Moses et al., 1995). Dopamine in the VTA is involved in anticipatory components of numerous motivated, reward-seeking behaviors including sexual behavior, feeding, and the administration of drugs of abuse (Blackburn et al., 1992; Blackburn et al., 1987; Blackburn et al., 1989; Damsma et al., 1992; Fibiger et al., 1992; Moses et al., 1995; Wenkstern et al., 1993; Wise, 2004; Wise, 2005). Direct pharmacological manipulations and opioid self administration studies in rats reveal opioids to be rewarding when infused into the mPOA and VTA (Agmo and Gomez, 1991; Agmo and Gomez, 1993; Agmo et al., 1994). In male rats conditioned place preference for ejaculation-induced reward is blocked by opioid antagonists injected directly into the mPOA (Agmo and Berenfeld, 1990). In songbirds as in mammals, VTA and mPOA share reciprocal neuroanatomical connections (Riters and Alger, 2004); and VTA projects directly to song control nuclei (Appeltants et al., 2000; Appeltants et al., 2002; Lewis et al., 1981). Thus, mPOA and VTA are ideally positioned to influence motivation and reward related to song production.

Involvement of dopamine in mPOA in directed and undirected song

Past studies of male starlings indicate that the mPOA is larger in sexually active males producing high rates of female-directed song compared to males singing high rates of undirected song (Riters et al., 2000). Neuronal activity in mPOA, as indicated using immunolabeling for immediate early genes, correlated positively with female-directed but not undirected song (Heimovics and Riters, 2005). Finally, lesions to the mPOA in male starlings suppressed female-directed song and other courtship behaviors (Alger et al., 2009; Alger and Riters, 2006; Riters and Ball, 1999) but increased undirected song production (Alger and Riters, 2006). These data suggest the mPOA stimulates female-directed but inhibits undirected song.

Studies using dopamine specific markers in songbirds support the idea that dopamine in mPOA differentially regulates female-directed and undirected song. The density of immunolabeling for tyrosine hydroxylase (TH; the rate-limiting enzyme for catecholamine synthesis) in mPOA correlated (negatively) with female-directed but not undirected song in male starlings ((Heimovics and Riters, 2008); Figure 2). (Labeling for the norepinephrine marker dopamine beta hydroxylase did not correlate similarly, indicating TH in this case reflected dopamine activity). D1 dopamine receptor densities in mPOA measured using autoradiography also correlated negatively with female-directed song, but positively with undirected song (Heimovics et al., 2009). Although site-specific dopamine manipulations and measures in the mPOA of songbirds are needed to understand the role of mPOA dopamine in directed and undirected song, the context-specific correlations between

dopamine markers and song suggest that the role of dopamine in mPOA differs depending upon whether song is female-directed or undirected song.

Although, studies have not been performed to measure dopamine release in mPOA during song, studies using microdialysis and site specific dopamine pharmacological manipulations in male rats and Japanese quail indicate that dopamine is released in the mPOA in association with sexually motivated behavior (Hull et al., 1995; Kleitz-Nelson et al., 2010b). Furthermore injection of dopamine D1 receptor antagonists directly into the mPOA in male Japanese quail and rats suppresses male sexual behavior (Kleitz-Nelson et al., 2010a; Moses et al., 1995). When paired with pharmacology data showing peripheral administration of a D1 dopamine agonist to stimulate female-directed song (Schroeder and Riters, 2006), these data suggest dopamine acting at the D1 receptor likely plays a stimulatory role in male sexually motivated song; however this remains to be tested. The role of dopamine in the mPOA in undirected song also awaits future research.

Involvement of dopamine in VTA in directed and undirected song

Studies using labeling for immediate early genes to identify neuronal activity also reveal positive correlations between labeling in VTA and female-directed song but not undirected song (Heimovics and Riters, 2005). Similarly, electrophysiological activity in VTA increased more in male zebra finches in association with female-directed than undirected song (Hara et al., 2007; Yanagihara and Hessler, 2006). Colocalization of immediate early gene and TH immunoreactivity correlated with female-directed song in male zebra finches (Goodson et al., 2009), and the density of TH immunolabeling in VTA correlated positively with female-directed but not undirected song in male starlings ((Heimovics and Riters, 2008); Figure 2), suggesting differences in VTA activity associated with female-directed and undirected song relate to differences in dopamine activity. Consistent with this idea, in male zebra finches dopamine release is highest during female-directed song compared to undirected song in area X, a striatal brain region that receives strong dopaminergic input from VTA (Sasaki et al., 2006). Finally, the role of dopamine in VTA in triggering directed vocal behaviors appears well conserved. For example, in rats both dopamine neuron specific lesions and dopamine antagonists administered to the VTA selectively reduced 50 kHz vocalizations (Burgdorf et al., 2007), vocalizations identified by Panksepp and collaborators as reflecting an anticipatory reward-seeking state (Knutson et al., 2002). Furthermore, dopamine agonists administered into the nucleus accumbens (a VTA projection region well studied for its involvement in reward) triggered 50 kHz vocalizations (Burgdorf et al., 2001).

Involvement of opioids in mPOA and VTA in directed and undirected song

In addition to pharmacological manipulations supporting a context-specific role for opioids in song (Riters et al., 2005; Schroeder and Riters, 2006), a study using immunolabeling for the opioid methionine-enkephalin (mENK) in male starlings suggests opioids in mPOA and possibly VTA are more closely linked to undirected song. Song was recorded from male starlings singing sexually motivated or undirected song (in the spring breeding season or nonbreeding season, respectively). When data from both seasons were combined, male song production correlated positively with mENK fiber density in both mPOA and VTA ((Riters et al., 2005) Figure 3 and 4). When data were analyzed by season a significant positive relationship was detected between mENK fiber density within mPOA and undirected song produced outside the breeding season, but not female-directed song produced within the breeding season (see regression lines in Figure 3). A similar trend ($p = 0.06$) was observed for VTA (Figure 3). Thus, these results suggest that enkephalin opioids in mPOA and possibly VTA are most closely linked to undirected song, a finding consistent with the idea

that undirected song may be more critically dependent upon immediate, intrinsic reward mechanisms than song that is sexually motivated.

In rodents, opioids and dopamine interact within the VTA to stimulate motivated behavior. Specifically, opioids within the VTA stimulate dopamine neuronal firing rate and release, and associated sexually motivated behaviors, presumably by inhibiting GABA which then disinhibits dopamine neuronal firing and release (reviewed in (Kalivas, 1993; van Furth et al., 1995b)). These effects appeared to be stimulated by activity of delta and mu opioid receptors but inhibited by activity at kappa receptors (Bruijnzeel, 2009; Kalivas, 1993). If in songbirds opioid activity at mu and delta receptors in VTA indirectly triggers dopamine release, then it is possible that opioids acting at these receptor subtypes (i.e., endorphin and enkephalin opioids (e.g., (Chang et al., 1980; Holtt, 1986)) in VTA will stimulate female-directed song. Indeed in rats, Burgdorf and collaborators (Burgdorf et al., 2007) demonstrated that mu opioid receptor agonists injected into VTA stimulated 50 kHz anticipatory vocalizations. In contrast, it could be that opioids acting at mu and delta receptors in mPOA will inhibit female-directed song given that opioids acting at these receptor subtypes in the mPOA inhibit male sexual behavior (Hughes et al., 1987; Kotegawa et al., 1997; Matuszewich et al., 1995; van Furth et al., 1995a). Effects of both site- and receptor subtype-specific opioid manipulations on birdsong are required to explore these predictions, especially given recent data indicating seasonal changes in opioid receptor subtype densities in songbird mPOA and VTA (Woods et al., 2010).

Summary: Homeostatic versus hedonic singing behavior

I argue here that the motivation to produce female-directed song may be unrelated to the intrinsically rewarding aspects of song production itself. Instead the successful attraction of a mate and the reward that accompanies physical interactions with the female or the act of copulation may provide the incentive for singing. Panksepp (Panksepp, 1998; Panksepp, 2005) has proposed that affective states are regulated through homeostatic mechanisms. Neurochemical deviations from a homeostatic equilibrium are perceived as unpleasant; whereas a return to homeostatic equilibrium is perceived as pleasant (Panksepp, 2005). The body of work reviewed here suggests that this model of homeostatic equilibrium applies to female-directed vocal communication. Opioid activity can be considered a “thermostat”. In the absence of social contact, opioid levels drop resulting in an unpleasant affective state which can be remedied through social contact induced opioid release. Thus a drop in opioid levels may trigger dopamine-mediated reward-seeking behaviors (such as female-directed singing). Once a male has attracted a female, opioids are released during physical contact, and dopamine-triggered seeking behavior is inhibited. This idea applies to other forms of directed vocal communication as well. For example, in birds, rodents, and primates opioid agonists suppress vocal behavior used by young animals to attract caregivers (another form of directed communication) (Carden et al., 1991; Carden et al., 1996; Herman and Panksepp, 1978; Kalin et al., 1995; Panksepp et al., 1978a; Winslow and Insel, 1991). Presumably, in the absence of a caregiver, opioid levels drop and the animal produces social contact vocalizations to attract a caregiver to restore opioid homeostatic equilibrium. Physical interactions with a caregiver then result in opioid release, triggering satiety and an inhibition of vocal behavior.

In the feeding literature, homeostatic feeding (i.e., feeding to meet nutritional needs) is contrasted with hedonic feeding (i.e., feeding for pleasure irrespective of homeostatic equilibrium (Saper et al., 2002)). Similar to hedonic feeding or the use of drugs of abuse, there does not appear to be any obvious, immediate external value to undirected song production. That is, in contrast to female-directed song, undirected singing results in no obvious social gain. If singing were controlled solely by homeostatic mechanisms there

would be no incentive for birds to sing undirected song because it does not evoke an obvious behavioral response in conspecifics. In the absence of an obvious external reward it is proposed here that that act of producing undirected song is intrinsically rewarded by immediate opioid release. The similarity of undirected song to hedonic feeding also extends to opioid involvement. Hedonic, but not homeostatic feeding is powerfully stimulated by opioids (Kelley et al., 2002; Saper et al., 2002). Similarly, undirected but not directed song is stimulated by opioids (Khurshid et al., 2010; Riters et al., 2005; Schroeder and Riters, 2006). In this scenario dopamine may also initiate song production but it is proposed that opioid reward triggered by the act of singing, maintains singing independent of its effects on the behavior of conspecifics.

Although opioids are proposed to underlie reward associated with both female-directed and undirected song, data indicate that opioid release inhibits female-directed song but increases undirected song (Khurshid et al., 2010; Riters et al., 2005; Schroeder and Riters, 2006) (but again see (Khurshid et al., 2010) for opposing results for female-directed song). Future research is necessary to determine how opioids can underlie reward associated behavior yet have such opposing effects; however, this idea is not unprecedented. For example, opioids are well known to underlie reward associated with both feeding and sexual behavior yet opioids stimulate feeding behavior (Glass et al., 1999; Gosnell et al., 1986; Morley, 1987) but generally play an inhibitory role in sexual behaviors (e.g., (Agmo and Paredes, 1988; Kotegawa et al., 1997; Maney and Wingfield, 1998; Riters et al., 1999; van Furth et al., 1995a)). The differential effects of opioids may be explained by opioids acting within distinct terminal regions, at distinct receptor subtypes or possibly reflect “dose-dependent” effects. For example, a relatively small opioid pulse associated with feeding or undirected singing may stimulate and maintain this behavior. In contrast, a large opioid pulse associated with copulation may result in sexual inhibition and temporary satiety.

Furthermore, future research is needed to determine the role of dopamine and opioids in song produced in contexts in addition to mate attraction and while in flocks. For example, in males directed song is also used to repel male conspecifics during territorial defense (Catchpole and Slater, 2008). It is possible that song that is used to repel other males may be negatively reinforced by removal of the male threat. To date in male European starlings D1 dopamine receptor density is found to correlate with male-male song within a subset of brain regions that only partially overlaps with those found to relate to female-directed song (Heimovics et al., 2009), suggesting partially distinct mechanisms underlie song within specific social contexts.

In sum, a growing body of data implicates dopamine and opioids in the regulation of song, and supports the idea that the role of these neurochemicals differs depending upon whether song is female-directed or undirected. The working hypothesis proposed here is that what rewards song differs depending upon the context in which song is produced, with undirected song relying more heavily on intrinsic reward (in part through opioids released in the mPOA by the act of singing) than song directed towards a female (which may be socially reinforced through opioids released as part of social interactions). Dopamine is proposed to regulate the motivation to sing within any context, however given the role of dopamine in sexual motivation and reward-seeking behavior it is expected that dopamine will play a predominant role in female-directed compared to undirected song.

Many of the theoretical underpinnings for the ideas discussed here are based on the influential publications of Panksepp (summarized in recent reviews (Panksepp, 2005; Panksepp and Moskal, 2008)) and his seminal textbook *Affective Neuroscience* (Panksepp, 1998). Panksepp proposes that evolutionarily conserved core affective neural systems underlie motivation, reward anticipation, and sensory pleasure that are vital to the pursuit of

activities crucial to survival and reproductive success. The studies reviewed here demonstrate that these concepts apply to topics as wide-ranging as birdsong and the motivation to communicate. Panksepp's development of the field of Affective Neuroscience shifted the understanding of emotional states in animals opening the way for studies of animal emotion, including the work reviewed here. Finally, in the tradition of Panksepp, it is expected that by understanding the neural regulation of context-appropriate communication in songbirds, we will identify manipulations that stimulate context-appropriate social interactions, which can be used in the design of clinical interventions in humans with deficits in the motivation to communicate.

Acknowledgments

Support from the National Institute of Mental Health R01 MH080225 is gratefully acknowledged. I also thank Bill Feeny for assistance with illustrations. Finally, I thank Dr. Jaak Panksepp whose body of research contributed substantially to the theoretical framework of this review.

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Figure 1.

Data demonstrating a stimulatory role for dopamine and an inhibitory role for opioids in female-directed song. Mean measures of song produced by male starlings after vehicle treatment (open bars) and treatment (dark bars) with A) the D1 dopamine receptor antagonist SCH 23390, B) the dopamine reuptake inhibitor GBR-12909, C) the opioid receptor antagonist naloxone, and D) the mu opioid receptor agonist fentanyl. *Indicates $p < 0.05$. See text for additional detail. Figures redrawn from Riters et al. (2005) and Schroeder and Riters (2006).

Figure 2.

Evidence that dopamine in mPOA and VTA is most closely related to female-directed song. Plots showing correlations between undirected (left) and female-directed (right) singing behavior and measures of tyrosine hydroxylase immunolabeling density in mPOA and VTA. Each point represents one individual. Presence of regression line indicates significant relationships ($p < 0.05$). See text for interpretation. Figures redrawn from Heimovics and Riters, 2008.

Figure 3.

Evidence that opioids in mPOA and possibly VTA are most closely related to undirected song. Scatterplots illustrating relationships between male song production (mean arcsine transformed number of minutes at which each male was singing) and mENK fiber density in mPOA and VTA. Each dot represents data from a single male. Black dots represent data from males observed singing undirected song outside the breeding season. Gray dots represent males observed singing female-directed song during the breeding season. For each scatterplot, the R^2 and thick black regression line are for the regressions performed on data from males singing undirected and female-directed song combined. The thin dark gray line is the regression line for males singing female-directed song (mPOA: $R^2 = 0.01$, $p = 0.80$; VTA: $R^2 = 0.20$, $p = 0.26$). The light gray line is the regression line for males singing undirected song (mPOA: $R^2 = 0.70$, $p = 0.009$; VTA: $R^2 = 0.53$, $p = 0.06$). See text for additional detail. Figures redrawn from Riters et al. (2005).

Figure 4.

Darkfield photomicrographs illustrating mENK fiber density in mPOA and the VTA of a male that did not sing and a male that sang at high rates. Arrows point to the boundaries of mPOA and VTA. TSM = tractus septomesencephalicus, v = ventricle, nIII = 3rd cranial nerve. Figure adapted from Riters et al. (2005).