

Linking vocal learning to social reward in the brain:

Proposed neural mechanisms of socially guided song learning

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The social environment plays an important role in vocal development. In songbirds, social interactions that promote vocal learning are often characterized by contingent responses of adults to early, immature vocalizations. Parallel processes have been discovered in the early speech development of human infants. Why does contingent social feedback facilitate vocal learning so effectively? Answers may be found by connecting the neural mechanisms of vocal learning and control with those involved in processing social reward. Here we extend the idea of Newman's social behavior network, a tightly interconnected system of limbic areas across which social behavior and motivation are distributed, to an avian social/vocal control network. We explore anatomical and functional overlaps between song circuitry and social-motivational circuitry. We find that circuitry linking basal ganglia with cortical areas serves to integrate social reward with vocal control and may underlie socially-guided vocal learning. In species that have evolved socially guided vocal learning, a unique link has been forged between social circuitry and vocal learning systems, such that learning is driven by social motivation.

## **Introduction**

Vocal learning, the ability to modify vocalizations as a result of experience with other individuals, is a rare phenomenon. Although the evolutionary lineage leading to humans diverged from that leading to songbirds 300 million years ago, the process by which birds learn to sing and humans learn to speak share parallels at multiple levels. Humans and songbirds must both achieve the complex task of learning to produce sounds which are functional for communicating with conspecifics. Song and language both require learning during a critical developmental period, and practice through immature vocalizations for both birds (subsong and plastic song) and babies (babbling).

An additional, and understudied, parallel is the powerful role of social feedback in the development of mature vocal forms. Evidence is rapidly accumulating that vocal learning in humans and songbirds is motivated by social factors and is intrinsically rewarding at the neural level. Functional and neural links between social-motivational brain regions and vocal learning circuitry continue to emerge from new investigations. Without social exposure, both humans and songbirds fail to develop normal vocalizations. Immature vocalizations play an essential role, not only in learning to use the vocal apparatus, but also in eliciting feedback from social partners to guide immature vocalizations into more mature forms. Our chapter will assess mechanisms of vocal learning with respect to the ecological contexts of young learners. A crucially important context, especially in altricial species, is the social environment.

Early work on vocal development across species found that, for both bird song and human language, learning primarily requires exposure to species-typical sounds during a sensitive period. Experimental manipulations found the amount of input necessary to be small, and effective regardless of the inclusion of social factors, provided that the learning organism

had extensive time to practice (i.e. Lenneberg, 1967; Marler, 1970). While this paradigm led to increased understanding of the neurological control of vocal production, researchers investigating the ontogeny of communication began to note that it could not explain all that they observed. Social stimulation, or lack thereof, can extend or delay the sensitive period for song learning in birds, or even allow vocalizations to be modified throughout life (Baptista & Gaunt, 1997; Payne & Payne, 1997). Different vocalizations may be utilized in different social contexts, and vocal learning does not merely involve learning to produce sounds, but also when and how to use them appropriately. If raised in an inadequate social environment, cowbirds may develop potent songs but not know how to use them (West et al., 1990), vervet monkeys may learn alarm calls but use them in response to non-threatening stimuli (Seyfarth & Cheney, 1986), and marmosets may learn vocalizations but fail to learn to take turns when communicating with conspecifics (Takahashi et al., 2016). While parrots may learn to mimic human speech through mere exposure, they can only learn to use language referentially and functionally when taught using socially interactive techniques (Pepperberg, 1993). Social partners may influence vocal development through a variety of mechanisms, providing learners with reinforcement, an attentional focus, general stimulation, or selective feedback.

Not all vocally learning species are equally socially influenced, necessitating a comparative, cross-species approach to understand what traits grant a given species the greatest capacity for vocal flexibility during ontogeny. Species with the most unpredictable environments, such as the zebra finches of central Australia, and the greatest mobility, such as migratory birds and mammals, tend to have the greatest capacity for learning new vocalizations and being influenced by social factors. This may be due to selective evolutionary pressures placed on species which would be most likely to encounter unfamiliar conspecifics with different

vocal dialects. Species which live in stable, consistent social groups year-round would gain less advantage from vocal plasticity, and are often less flexible vocal learners (Snowdon & Hausberger, 1997). The developmental mechanisms underlying the incorporation of social information into learned vocalizations also vary depending on a given species' ontogeny, sensitive periods, life history, social structure, access to vocal tutors early in life and, crucially, usage of vocalizations. Bird species which use song primarily for defending territories from competitors, and therefore benefit most by learning songs directly from dominant males, should be expected to learn song very differently from those who use song only for attracting a mate, and may benefit most from paying attention to which songs are most arousing to the opposite sex.

In the study of bird song development, two primary models of learning processes have been proposed: instructive and selective (Changeux et al., 1984; Jerne, 1967). Instructive models propose that stimulation from the environment adds information not already present in the behavioral repertoire. Instructive models typically consist of young birds listening to a tutor's song, memorizing it, and subsequently practicing until they can reproduce the song (e.g. sensorimotor learning; Konishi, 1965). Selective models propose that learning consists of experience leading to the selection and attrition of behaviors from a relatively vast pre-existing repertoire. The best known example of selective learning is "action-based learning" (Marler, 1991), also called "selective attrition" (Marler & Peters, 1982). Primarily studied in territorial sparrows, action-based learning refers to the selection of songs from a large, overproduced repertoire sung during the plastic stage of song learning. When territorial male sparrows engage in counter-singing, they exchange similar song types. During these social interactions, matching songs may be reinforced, while non-matching types are discarded (Marler & Nelson, 1993).

Young song sparrows are more likely to select matching songs from tutors they can overhear interacting with other birds than from those with which they can directly interact, and do not learn preferentially from more aggressive or higher-quality adults (Akçay et al., 2014; Beecher, 2016). While both instructive and selective models explain numerous aspects of song learning, especially the eavesdropping-based (Beecher et al., 2007) song learning strategy in territorial sparrows, both models rely heavily on imitation. Neither explains invention and improvisation of new song types which vary from that of the tutor, or the learning process of any species which utilizes non-vocal feedback or otherwise develops without exposure to an auditory model. The socially guided learning (SGL) model instead proposes that social partners may selectively reinforce components of immature vocalizations. Much like action-based learning, SGL relies on behavioral shaping, allowing an animal to retain those behaviors most often associated with a positive social response, but rather than relying on selective attrition of non-functional songs, SGL allows young learners to construct mature vocalizations from component sounds. When attempting to write an essay, we find it far easier to be given a blank page and construct the essay using our vocabulary rather than being given a list of all possible combinations of all possible words and whittling it down to only those words we wish to include. In the same way, it is easier for a developing organism to construct an adaptive vocalization from basic parts than by being born already able to produce all possible vocalizations and removing those elements which are non-functional. While action-based learning incorporates aspects of SGL, it only allows for social shaping through selective attrition, not the constructive mechanisms we propose.

### **Socially Guided Learning in Birdsong Function and Development**

There exist over 4000 species of songbird (oscine), and no two are precisely alike in ecological niche, life history strategy, or song learning trajectory. The degree of social

interaction necessary and sufficient for normal vocal development varies across species. Song serves two primary functions in birds: to declare a territory from which other birds are aggressively excluded, and to attract members of the opposite sex for mating (Catchpole & Slater, 1995; Kroodsma & Miller, 1996), though some species employ only one of these song functions. In many species of songbird only males sing, though there are numerous species in which females also produce song (Odom et al., 2014). There is extreme diversity in the types of songs birds produce, and each individual species has a characteristic acoustic structure. The simplest unit of the song is referred to as an ‘element’ or ‘note’. A series of elements that regularly occur together form a song ‘syllable’, while a sequence of multiple syllables that repeatedly occurs in a song is described as a ‘motif’ (Brenowitz et al., 1997) (see Figure 1). Most juvenile songbirds fail to develop normal song if they do not hear the song of a conspecific adult tutor, or if they cannot hear themselves sing.

Songbirds may be divided into ‘open-ended’ and ‘close-ended’ or ‘age-limited’ learners (Nottebohm, 1993). Open-ended learners, including canaries (*Serinus canarius*), red-winged blackbirds (*Agelaius phoeniceus*), and European starlings (*Sturnus vulgaris*), can continue to learn new songs or song elements for many years or throughout life (Adret-Hausberger et al., 1990; Yasukawa et al., 1980). For close-ended learners, song acquisition is restricted to a short sensitive phase, usually early in development. Research on vocal learning in birds has been guided by the sensorimotor model, based on studies of song learning in the white-crowned sparrow (*Zonotrichia leucophrys*), a close-ended learner (Konishi, 1965). This model incorporates two developmental stages: the sensory period, during which the song is acquired and memorized, and the sensorimotor period, during which the bird practices the song and uses auditory feedback to compare its own song to its stored memory. The beginning of the

sensorimotor phase is accompanied by the production of *subsong*, the first song-like vocalizations, but which are unstructured, vary from moment to moment, and bear little resemblance to adult song (Sound File 1). Its variability invites comparison with the early stages of babbling in human infants. Subsong and baby babbling both serve to train the vocal apparatus and improve vocal control, as well as to elicit social feedback to facilitate development of more mature sounds (Goldstein et al., 2003). Subsong gradually develops into *plastic song* that incorporates recognizable syllables from the song model (Sound File 2), but remains variable and requires additional practice before it will mature into the final, *crystallized* adult song (DeWolfe et al., 1989) (Sound File 3). Syllable structure tends to reach an adult form prior to the onset of crystallized syntax, such that even after learning to produce mature and stereotyped song elements, young birds will still rearrange the sequence of these elements between song bouts. The crystallization process is rapid compared to the prolonged learning period preceding it (Todt & Geberzahn, 2003). The duration of the sensitive period is not fixed, but may vary depending on social experience. For many species, raising birds in isolation extends the sensitive period, such that adults may still learn song elements when a tutor is finally presented (Slater et al., 1988). For some species, birds exposed only to the song of a different species during development will continue to learn songs from conspecifics at a time when normally-raised birds can no longer learn new song (Slater et al., 1988). Insufficient social experience or exposure to the tutor leaves the brain open to learning for longer than normal.

The subject of sensitive periods in the development of song has led to some debate on the differing effects of tutoring birds using live, interactive social partners versus pre-recorded tapes of birdsong. There are a few oscine species in which naïve individuals may produce near-perfect copies of tape-recorded song, including chaffinches (Thorpe, 1958) and white-crowned sparrows



(Marler, 1970), which were among the first and most commonly studied model species. Under natural conditions, these species learn via eavesdropping on neighboring adult males while establishing territories (Beecher et al., 1994; Nice, 1943). It is important to note, however, that social influences can dramatically change song learning, and white-crowned sparrows still learn more readily from a live tutor than a recording (Baptista & Petrinovich, 1984). Early tape-tutoring isolate studies concluded that white-crowned sparrows uniformly reject heterospecific song (Marler, 1970), but when the tutor is a live bird they will learn from another species (Baptista & Petrinovich, 1984). Furthermore, while conspecific tape-tutored songs are deemed 'normal' to the ears of researchers, they are often functionally useless. A study of tape-tutored wood thrushes (*Hylocichla mustelinu*) concluded that they developed normal wild-type song, but when the song was played back to wild wood thrushes they failed to elicit any response (Lanyon, 1979). Many other species fail to learn normal song entirely when solely exposed to tape recordings (Baptista & Petrinovich, 1986; Deregnaucourt, et al., 2013; Thielcke, 1970). Facultative social learners can use recordings to form a song model memory in isolation, but their learning is greatly improved with exposure to a live tutor. Indigo buntings (*Passerina cyanea*), domestic canaries, and European starlings can all learn a few syllables from a recording, but learn far more when exposed to the same song produced by a live tutor (Chaiken et al., 1993; Rice & Thompson, 1968; Waser & Marler, 1977). Obligate social learners, such as Eurasian tree-creepers (*Cethia familiaris*) and North American sedge wrens (*Cistothorus platensis*)<sup>1</sup>, do not learn from tape recordings, but will readily learn from one another when naïve individuals are housed together (Kroodsma & Verner, 1978; Thielcke, 1984). Human infants seem to be subject to similar learning constraints, as studies of children raised in isolation found that they fail to develop speech normally (Fromkin et al., 1974; Lane, 1976). It is important to

remember, however, that when a social organism such as a human or songbird is raised in isolation it is deprived not only of normal exposure to vocalizations but also of all typical social exposure. As in the case of isolate-reared monkeys developing severe behavioral abnormalities (Harlow & Harlow, 1962), early social deprivation likely has dramatic developmental impacts beyond vocal learning.

The impact of social factors also seems to shift over the course of development. For example, white-crowned sparrows will readily learn from a tape recording until 50 days of age, but will only accept live tutors as song models past that point (Baptista & Petrinovich, 1986). Conversely, starlings learn better from live tutors than tapes at 4 months of age, but tape tutoring becomes more effective by 12 months (Chaiken et al. 1993). A possible reason for this variation may be the difference in the repertoire sizes of these two species. White-crowned sparrows rarely sing more than one song as adults (Baptista, 1975), while starlings can sing dozens of different song types (Van Hout et al., 2012). This may impose different constraints on learning, such that it becomes too restrictive for a species with a large repertoire to limit learning to only one familiar tutor.

### **Socially Guided Vocal Learning in the Zebra Finch**

Each oscine species has its own learning requirements and capabilities, and no single species can serve as a model of vocal learning for all oscines. However, the species which has been most thoroughly studied and whose learning mechanisms have been most often compared to those of humans is the zebra finch. For this species, live social interaction of the correct form and timing is vital for normal song learning. Zebra finches (*Taeniopygia guttata*) are highly gregarious, non-territorial, and socially monogamous, using their song solely for the purpose of mate attraction and pair maintenance. Only males sing, and preferentially use the song of their

own father as a learning model. Zebra finches raised in isolation develop a song with abnormal properties, including unusual note structure and decreased stereotypy (Price, 1979; Williams, Kilander & Sotanski, 1993). Isolated males often fail to develop a canonical motif, and will only rarely repeat a given sequence of notes. Untutored songs also often include repeated notes, resembling the structure of the trills of canaries (Williams, 2004). While these abnormalities may arise due to the absence of a song model normally provided by a tutor, some features of untutored song appear to arise due to the absence of behavioral feedback from conspecifics.

The zebra finch sensory period lasts from approximately 20-65 days of age, while the sensorimotor period lasts from days 35-90 (Brainard & Doupe, 2000), though young finches deprived of social interaction during the sensitive period will continue to be able to learn for at least several weeks beyond the normal close of the sensitive period (Clayton, 1987; Eales, 1985). Zebra finches require minimal exposure to the tutor song, and can learn to sing well with less than a minute of interactive tutoring per day (Tchernichovski et al., 1999). Sensory responses to songs are traditionally thought to be fixed and immutable, but are increasingly understood to be modulated by prior experience (Gilbert et al., 2009; Thompson & Gentner, 2010). Neural responses to songs are strongly modulated by whether or not they are reinforced by food or social feedback, and differences in acquired salience predict learning rate (Bell et al., 2015). Throughout song development, zebra finches are naturally exposed to a highly social environment, which favors a function for listeners in song learning. In the gregarious brown-headed cowbird (*Molothrus ater*), female cowbirds selectively respond to immature male vocalizations with a non-vocal signal, in the form of a rapid lateral wing movement called a ‘wing stroke’. Juvenile males attend to these cues, which are believed to be indicators of female arousal, and repeat elements which elicited a wing stroke, allowing female listeners to direct the

course of song learning (West & King, 1988). Similar mechanisms may influence learning in zebra finches which, like cowbirds, are highly gregarious and experience a high degree of overlap in the sensory and sensorimotor phases of song learning (Roper & Zann, 2006; Slater et al., 1988), allowing the opportunity for social feedback to influence learning. As with buntings, canaries, and starlings, for zebra finches interaction with a live tutor leads to more effective song learning than passive exposure to a tape-recorded song (Chen et al., 2016; Deregnacourt et al., 2013; Eales, 1989). The salience of adult tutor song is based on physical proximity of the tutor (Mann & Slater, 1995), aggression directed towards the fledglings (Clayton, 1987; Jones & Slater, 1996), the tutor's mating status and partner quality (Eales, 1987; Mann & Slater, 1994), visual cues such as color morph (Mann, 1991; Mann & Slater, 1995), and auditory information such as song similarity between the father and subsequent song tutors (Clayton, 1987).

Juvenile males preferentially learn to sing from their fathers, even when other potential tutors are available, although they will learn from alternative tutors depending on the level of parental care they receive (Williams, 1990). Zebra finches cross-fostered under Bengalese finches (*Lonchura striata*) will produce a good copy of their foster-parent's song, even if a zebra finch model is available in a neighboring cage (Bohner, 1983; Immelmann, 1969). Price (1979) hand-reared zebra finches such that they imprinted on him, and then tutored them each time he fed them by playing an adult song from a tape-recorder hung around his neck. The finches learned only a few syllables from the recording. However, if a finch can control the delivery of a recorded song by pressing a key, causing presentation of the model to be contingent on their own actions, they can learn to produce a good imitation (Adret, 1993). Control over the stimulus, much like interaction with a live tutor, may increase the young bird's attention to the song, leading to better learning. Simply pairing a stimulus with the sound of the model might

sufficiently enhance motivation or arousal to improve learning, as in the case of common nightingales (*Luscinia megarhynchos*) which will only learn a taped song when they can observe the researcher operating the loudspeaker (Todt et al., 1979). Furthermore, male siblings have an effect on song learning, as multiple male zebra finches raised together by the same father will develop a highly variable song compared to that learned by a male without siblings (Tchernichovski & Nottebohm, 1998).

As in the brown-headed cowbird, non-singing female listeners are also known to affect song learning in the zebra finch (Jones & Slater, 1993). Males raised with deaf adult females sing more frequently and develop more atypical songs than those raised with hearing females (Williams, 2004), and blindfolded males raised with a tutor develop more accurate song when also raised with a female sibling than without one (Adret, 2004). These cases of enhanced learning in the presence of conspecifics may be the result of heightened arousal or attention in social contexts (ten Cate, 1991), or the result of attendance to song-elicited conspecific behaviors (Vyas et al., 2009). A recent discovery shows that zebra finch females may guide juvenile male song learning in a manner very similar to that seen in cowbirds, by selectively responding to more mature, complex, or arousing elements with a wing stroke (Menyhart et al., in prep). These movements are extremely rapid, lasting less than 0.3 seconds and imperceptible to the human eye, only visible when video-recorded and then played back at 30% speed. This may explain the failure of earlier efforts to determine what cues may be responsible for differing trajectories of juvenile song learning in the presence of females; past studies observed live zebra finches at real speed, such that their rapid cues could not be detected (e.g., Houx & ten Cate, 1998). This bias towards using human perceptual capacities to observe avian interactions has led to many interesting behaviors being overlooked in the past. Among the manakins, a South American

group of birds known for their spectacular courtship displays, the black manakin (*Xenopipo atronitens*), was thought to have a simple and lackluster display, with a courtship routine consisting only of repetitive hopping (Kirwan & Green, 2012). However, when the display of the black manakin was captured on high-speed video and slowed down, it was discovered that every “hop” was a very rapid (360 ms) and technically complex backwards summersault (see Lindsay et al., 2015). But if these movements are too rapid for humans to perceive, might they also be too quick for birds to perceive, much less use as a social cue to alter their own behavior? The golden-collared manakin (*Manacus vitellinus*) also has a very fast courtship display, which consists of mechanical sounds and rapid lateral leaps between sapling trunks. High-speed video revealed that prior to each leap, the male quickly flares his neck feathers into a ‘beard’, an action that takes an average of 53 milliseconds (Fusani et al., 2007). The timing of this beard-up motion has the highest rate of inter-individual variability of any aspect of the complex display, and is also the primary basis upon which females decide whether or not to copulate with a given male (Lainy Day, personal communication). At least in some avian species, individuals are able to both perceive and make behavioral alterations based on extremely rapid movements of conspecifics, far too fast for a human researcher to perceive unaided, as human visual system critical flicker fusion rate is about half that of a small bird (Healy et al., 2013).

### **Song Control Circuitry in a Social Brain**

Until recently, social behavior in the brain was thought to be divided into distinct nodes, each of which was the center for a particular category of social behavior, such as parental care, territoriality, or pair-bonding. An alternative model proposed by Sarah Newman (1999) instead suggested a social system network, a tightly interconnected system of limbic areas across which social behavior and motivation are distributed. Social behaviors are not localized to a particular

area, but rather neural activity distributed in a certain way across the network generates a given behavior. Exactly what stimulus is necessary to elicit a behavior and how it manifests in the brain varies by species, sex, age, and life history traits such as gregariousness and territoriality. This social circuit overlaps significantly with the circuitry governing motivation and reward, in particular the amygdala, which mediates motivational arousal. The connection between the amygdala and ventral tegmental area (VTA) makes up much of the mesolimbic dopamine pathway modulating the behavioral response to rewarding or motivating stimuli (Syal & Finlay, 2011).

Before delving into the neurobiology underlying song learning and production, it is helpful to conceptualize the tasks the brain must accomplish in order to drive vocal learning. First, it must generate motor commands to the vocal organ (the syrinx). It must also modify these commands in response to auditory feedback (i.e. the bird detecting that its own song is not a match to its memorized model) or social feedback (i.e. behavior from a conspecific updating the bird's mental model of ideal song). This requires the brain to use feedback to evaluate song performance, then alter motor output to minimize the difference between the song and the ideal model (Mooney, 2009). Finally, the brain must motivate the bird both to sing and to adjust its song based on feedback, requiring some form of reward resulting from singing behavior and accurate matching responses to auditory and social feedback. How the brain accomplishes the comparison between song output and the mental model of ideal song is still being investigated, but the neural mechanisms for song production and variability are better understood. Exploration of the neural circuitry underlying song behavior, plasticity, and variability may shed light on how this machinery incorporates social feedback into song learning.

Song behavior and learning is regulated by an interconnected network of discrete brain nuclei referred to as the song system, which distinguishes the songbird brain from that of birds which do not learn to vocalize (Kroodsma & Konishi, 1991; Wild, 2004). During song learning, these nuclei undergo anatomical and neurochemical changes (Alvarez-Buylla & Kirn, 1997). This network is composed of two pathways: the song motor pathway (SMP) and the anterior forebrain pathway (AFP), which together affect vocalizations through the muscles of the respiratory system and the syrinx (Figure 2). The SMP is a posterior motor pathway connecting nucleus RA (robust nucleus of the arcopallium), HVC (proper name, not an acronym; previously ‘high vocal center’), and nXIIts (tracheosyringeal portion of the 12th cranial nerve). Each of the precise individual functions of these regions is a matter of some debate, as discussed below, but together these connected regions control song production and some aspects of song learning. Lesions in the SMP will disrupt or entirely abolish singing (Simpson & Vicario, 1990). In contrast, the AFP is involved in evaluation of the bird’s song via auditory feedback and adaptive modification of the song, and is essential to both song learning and recognition (Brainard & Doupe, 2000). Lesions to this pathway will not immediately degrade crystallized song, but will prevent accurate vocal learning by reducing song variability and plasticity (Bottjer et al, 1984; Olveczky et al., 2005). The AFP is an anterior cortical-basal ganglia-thalamic loop originating in HVC, which then projects to Area X of the paraolfactory lobe and LMAN (lateral magnocellular nucleus of the anterior neostriatum), ultimately connecting back to the motor pathway at RA (Doupe et al., 2005). Nuclei in the AFP, as well as its connections to the SMP, regress substantially by the time the sensitive period closes (Hermann & Arnold, 1991; Iyengar et al., 1999). The linkage between these two pathways, as well as the fact that both contain neurons which respond both to song production (Leonardo & Fee, 2005; McCasland 1987) and auditory



or social stimulation (Margoliash, 1983; Vicario & Yohay, 1993; Yanagihara & Hessler, 2006), suggests a mechanism by which social feedback in response to a juvenile's song may influence vocal output.

### **The Song Motor Pathway: The Vocal Generator**

A shared characteristic of human speech and birdsong, but not the majority of other animal vocalizations, is that they are controlled by the telencephalon. In birds, the anatomical basis of this control is the SMP. The nucleus HVC is a target for auditory and motor pathways, and conspicuously a shared component of the SMP and AFP. The size of HVC is also altered by social factors, as birds placed in a complex social environment develop a larger HVC than those housed with a single conspecific (Lipkind et al., 2002). This differential growth occurs despite the fact that birds in the simple social context sing far more than those in the complex context, indicating that it is caused not by vocal output levels but instead by the task of processing a rich auditory environment (Adar et al., 2008). HVC's position as a nexus connecting various circuits in the sensorimotor system makes it a good place to begin investigating song circuitry in social context.

HVC seems to function as a neural clock, firing in time with the elements of the song and generating its tempo. Singing-related activity in the SMP propagates through the system, arising in HVC prior to RA (McCasland, 1987). HVC firing activity is time-locked to individual syllables, but given that stimulation of HVC disrupts song (Ashmore et al., 2005) and that HVC activity is present even in deaf birds (McCasland & Konishi, 1981), it seems to serve a strictly motor rather than auditory function. HVC neurons projecting to RA rarely fire an action potential unless the bird sings, and even then the firing is very brief (about a 10 millisecond burst at a

single point during a 1 second motif) (Hahnloser et al., 2002). Ablation of HVC neurons projecting to RA, but not those projecting to Area X, will severely degrade the structure of the song (Scharff et al., 2000). This indicates that motor commands from HVC proceed directly to RA without passing through the AFP. Different neurons fire at different time points in the motif, suggesting that these neurons function to specify the production timing of different song elements. Given that some of the neurons also fire during intervening gaps of silence, they may also specify the timing of inter-note temporal spacing. In line with the idea that HVC controls song tempo, when HVC is cooled down the tempo of all aspects of the song, from individual notes to the entire motif, slow down by about 3% per degree Celsius of cooling (Long & Fee, 2008). Surprisingly, cooling has little effect on any other aspects of the song, such as amplitude or pitch. Cooling RA has little discernable effect on any aspect of song. It is possible that RA simply serves to turn HVC's timing signal into a motor signal, specifying the acoustic features of the song (like the structure of syllables) which should be produced according to the timing HVC specifies.

### **The Anterior Forebrain Pathway: Learning and Variation**

As previously mentioned, the effect on song of lesioning components of the AFP is dependent on the developmental time at which it occurs. After song has crystallized, AFP lesions seem to have little immediate effect on song in most contexts. Lesions during song learning, however, prevent normal adult song from being fully learned, instead resulting in song with abnormally high stereotypy which never progresses beyond that point, as if premature crystallization has occurred (Scharff & Nottebohm, 1991). Neural activity in the AFP during singing is strongly modulated by the presence of a conspecific listener. The magnitude and variability of activity in LMAN and Area X are lower and more consistent during singing

directed to a female than undirected singing produced when the male is not oriented toward another conspecific (Hessler & Doupe, 1999a). LMAN seems to be the song's 'jitter injector', inserting variability into song during sensorimotor learning, thereby ensuring that the juvenile bird explores its acoustic range (Kao & Brainard, 2006). Stimulation of LMAN during singing will cause perturbation of the song, while LMAN inactivation reduces the bout-to-bout variability of plastic song (Oliveczky et al., 2005), resulting in a repetitive and stereotyped song. The firing rate of LMAN neurons changes over developmental time, with their highest rate occurring during sensorimotor learning, suggesting that developmental change in song variability is a direct result of changes in LMAN activity. Supporting this idea, stimulating LMAN alters song structure almost immediately (as early as 30 milliseconds after stimulation) (Kao et al., 2005). LMAN was once thought to mediate song plasticity based on auditory feedback of the bird's own song as it attempted to match the song 'template' – the mental representation of the precise form of the memorized song of the tutor – yet LMAN neurons are entirely unresponsive to manipulated auditory feedback, suggesting that in LMAN the bird's own song is not used for error detection (Leonardo, 2004). Much like RA, LMAN serves a motor function, as neural activity in LMAN increases during song production (Hessler & Doupe, 1999b) and persists in deafened birds. Localized cooling of LMAN, much like HVC, slows down the timescale of subsong (Aronov et al., 2011). The timing signal from HVC, coupled with the 'noise' added to the signal from LMAN, may work in concert to deliver a precise motor pattern to the vocal muscles via RA.

It remains unclear whether LMAN is simply acting permissively to allow vocal plasticity, or if it is truly providing an instructive signal by injecting noise. Despite the differing level and timing of activity in LMAN between directed and undirected singing, the average pattern of

firing for an individual neuron is similar across these social contexts (Kao et al., 2008). Furthermore, stimulating a single locus of LMAN will consistently change a targeted syllable in the same way, for example always increasing its pitch, rather than inserting variability at random (Kao et al., 2005). Rather than simply driving variation, LMAN may be systematically biasing acoustic output, instructively driving vocalizations toward a particular goal. When a finch is negatively reinforced by a burst of white noise in response to a particular syllable exceeding a certain pitch threshold, the bird will shift the syllable's pitch downwards (Sober & Brainard, 2009; Tumer & Brainard, 2007). Inactivation of LMAN will cause the syllable to instantly revert to its original pitch (Andalman & Fee, 2009). LMAN thus appears to be actively biasing song away from vocal errors.

Although the influence of the AFP on song is more obvious during song learning, it continues to regulate song variability in adults. After song crystallization, AFP activity and acoustic variability are higher during undirected song than directed song (Jarvis et al., 1998; Sossinka & Bohner, 1980), with more variable spike timing during undirected song (Kao et al., 2008). Lesioning LMAN will abolish this social-context-dependent variability (Kao & Brainard, 2006), but does not prevent a male bird from performing other courtship-related behaviors normally produced only in the presence of a female, such as dancing and beak wiping. Because males seem to be able to interpret female social cues in the absence of LMAN, their capacity to detect and respond to social context must lie elsewhere in the brain and selectively activate LMAN when a female is not present.

The role of Area X in song learning remains as mysterious as its cryptic name implies, with conflicting findings thus far. Neurons in Area X exhibit highly variable patterns of firing during singing, leading some investigators to suggest that they may drive variability downstream

in LMAN (Goldberg et al., 2010). Conversely, and in contrast to lesions of LMAN, juveniles with Area X lesioned exhibit normal vocal variability (Goldberg & Fee, 2011; Sohrabji et al., 1990). However, eliminating Area X leads to protracted variability in adult song, with abnormal acoustic structure and little resemblance to the song of the tutor (Scharff & Nottebohm, 1991). It has also been proposed that Area X is the site where the song template is stored and compared to the bird's own song output. This 'AFP comparison hypothesis' posits that auditory information about the bird's own song is transmitted to Area X, where it is evaluated against the template (Mooney, 2004; Sakata & Brainard, 2008). If this is the case, Area X neurons should respond to vocal errors while birds are singing, but distorted auditory feedback does not elicit such responses (Kozhevnikov & Fee, 2007; Leonardo, 2004). Furthermore, singing-related activity in Area X is not altered by deafening the bird (Hessler & Doupe, 1999a), contrary to what one would expect if the region was sensitive to perceived auditory error. The AFP comparison hypothesis is motivated largely by observations of AFP activation in response to auditory stimuli in birds while not singing, anesthetized, or asleep (Dave & Margoliash, 2000; Doupe, 1997; Prather et al., 2008). However, response to auditory input is ubiquitous throughout both the AFP and SMP in non-singing birds, even in syringeal motor neurons, and is not a special property of Area X (Fee & Goldberg, 2011; Williams & Nottebohm, 1985). These observations led Fee and Goldberg (2011) to hypothesize that Area X does not store the song template, evaluate match to tutor, process auditory feedback, or receive an error evaluation signal from elsewhere in the AFP. Rather, Area X may receive an evaluation signal conveying the quality of song as it is produced via neuromodulatory inputs. Particularly well suited to carry such a global, rapid (<100 milliseconds), and time-dependent signal indicating good or bad vocal performance is the dopaminergic system, as discussed below.

## **Reward Value of Song: Plugging in to Social Circuitry**

A great deal of effort has been made to map out which neural circuits are involved in various social behaviors such as sexual behavior, aggression, and parental behavior. Studies of these regions have often led to the unexpected conclusion that there is considerable overlap in the circuitry required for these behaviors, leading to exploration of the possibility that they form an integrated social behavior network, much like the song learning network. Newman (1999) proposed a system in mammals consisting of six limbic areas, each identified as regulating multiple social behaviors, and each reciprocally connected to each of the others (Figure 3). Rather than a single region regulating a single social behavior, each region responds to a number of stimuli. Social context leads to a distinct pattern of activation across regions, and this determines behavioral response. Evidence increasingly suggests that this network exists in all vertebrates, and some of the most relevant findings come from birds (see Goodson, 2005), with network responses to social stimuli differently patterned in species of songbird with different levels of sociality (Goodson et al., 2005). The social behavior network is also reciprocally connected to the mesolimbic reward system, enabling social decision-making, which requires evaluation of the salience of a given stimulus before a behavioral response is executed (O'Connell & Hofmann, 2011). In order to determine the neural mechanisms by which social feedback may be affecting the trajectory of song learning, we must establish a) that singing is rewarding, activating the mesolimbic reward system, b) that social context modulates this reward value, and c) that the social-motivation system is connected to the song system and modulates its activity.

We know that song learning and singing behavior are controlled by the neural song system, and that both are affected by social factors. However, we know little about how social

reward and song circuitry are linked. Reward associated with certain behaviors can act as a powerful incentive to perform those behaviors, and can influence food intake, copulation, and social interaction (Agmo & Berenfeld, 1990; Berridge & Kringelbach, 2008). For a socially gregarious species like the zebra finch, motivation to seek social affiliation is important for survival, attention to social feedback during development is necessary for learning a reproductively successful song, and attention to social context in adult males is vital for attracting a mate. Given that songbirds are motivated to produce song at high rates in multiple social contexts, it is likely that singing is linked to reward. In humans, adults exhibit robust fMRI activation in the ventral striatum – a region involved in reward processing – when successfully learning new words, suggesting that language learning is intrinsically rewarding (Ripolles et al., 2014). The idea that vocalization is intrinsically rewarding has also been investigated in a non-oscine bird, the ring dove (*Streptopelia risoria*), in which male courtship involves cooing to a female. Estrogen then acts on the midbrain song nucleus (mICo) of the female, inducing her to coo in response (Cohen & Cheng, 1981). The female's coo, not the male's, causes an endocrine cascade in the female which results in egg-laying (Cheng, 2003). In order to investigate whether song is intrinsically rewarding in songbirds, Riters and Stevenson (2012) used a conditioned place preference paradigm to assess the reward value of singing directed (at a social partner) versus undirected song. When placed in an apparatus with two distinctive sides, male zebra finches preferred to spend time on the side where they had previously produced undirected song, suggesting that singing is coupled with reward state. They displayed no preference for the side of the apparatus in which they had previously sung directed song. This indicates that the role of reward in song production differs depending on social context, with directed and undirected song relying on different mechanisms of reward. Directed song is likely externally reinforced by

conspecifics, with the associated reward value resulting from successful social feedback elicitation, mate attraction, or copulation. In line with this hypothesis, males that produced directed song but failed to attract a female developed an aversion to the side of the apparatus where they had sung. Ritters and Stevenson suggest that production of undirected song, without immediate social reinforcement, may instead rely on an intrinsic reward system and the act of producing undirected song could activate neural reward systems. However, in light of work suggesting that undirected song also serves a communicative purpose for more distal recipients, this hypothesis may need to be revisited (Dunn & Zann, 1996). What mechanisms might underlie the reward value of song, and how is it modulated in different social contexts?

A leading candidate for the cause of context-dependent neuronal activity in the AFP is dopamine, a catecholamine neurotransmitter and an important contributor to the neural mechanisms allowing animals to pursue reward (Koob, 1996). Goal-directed, socially motivated vocal behaviors, such as ultrasonic vocalizations in rats anticipating a social reward, can be stimulated by dopamine (Wintink & Brudzynski, 2001). In songbirds, dopamine plays a primary role in sexually motivated song directed towards females (Heimovics et al., 2009), and peripheral injections of dopamine agonists stimulate song produced in response to the introduction of a female, whereas antagonists inhibit song (Rauceo et al., 2007; Schroeder & Ritters, 2006). Song produced in a social context appears to be highly rewarding, as elevated dopamine levels in the striatum of birds during directed singing resemble those after drug administration in mammals (Sasaki et al., 2006). The neural song system is strongly innervated by catecholaminergic neurons (Appeltants et al., 2001; Liao et al., 2013), which is not seen in comparable forebrain areas in bird species which do not sing (Moons et al., 1994). Catecholaminergic innervation of



the song system is also much stronger in male zebra finches than in non-singing females (Bottjer, 1992).

Dopamine also contributes to behavioral reinforcement that mediates appetitive learning (Panksepp & Moskal, 2008). Dopaminergic neurons in the VTA (a mesolimbic region) of monkeys trained on an operant task encode discrepancies between the expected reward normally delivered to them following a conditioned stimulus, and whether or not the reward is actually delivered (Schultz et al., 1993). Intense social interactions also result in increased glutamate activity in VTA (Huang & Hessler, 2008). In the zebra finch, EGR-1 expression in catecholaminergic neurons in VTA is significantly higher in birds which have been tutored socially than in untutored and passively tutored birds, suggesting that it is social interaction, not merely hearing song, that leads to activity in VTA (Chen et al., 2016). In songbirds, VTA is a primary source of dopaminergic input to both LMAN and Area X (Gale & Perkel, 2006; Lewis et al., 1981), where it also regulates synaptic plasticity (Ding & Perkel, 2004) and may encode prediction errors in song production. VTA neurons are known to exhibit singing-related activity, and projections from VTA to the song system modulate early gene activity related to social context (Hara et al., 2007). Dopamine levels in Area X are elevated more during directed song than undirected song (Sasaki et al., 2006), and infusion of dopamine antagonist near Area X (though possibly also affecting LMAN) increases variability during directed song (Leblois et al., 2010), hinting that dopamine may function as a regulator of AFP activity. Given that more than 95% of Area-X projecting VTA neurons are dopaminergic (Person et al., 2008), changes in VTA activity likely affect the release of dopamine in the AFP, leading to changes in song output and variability. When perceived song quality is distorted with auditory feedback, VTA neuron activity is repressed, encoding this performance error (Gadagkar et al., 2016). Therefore, when a

bird makes a vocal ‘mistake’ which does not match the memorized tutor song, or fails to elicit a wing stroke or other positive feedback from a conspecific, VTA neurons may detect this error and modulate song away from it. This idea is supported by the finding that lesions of dopaminergic inputs to Area X greatly impair vocal learning in the Bengalese finch, while having no detectable effect on vocal performance (Hoffmann et al., 2016).

Particularly among neuroscientists, song learning and the reward value driving it is considered strictly internally computed, the sole result of the young bird comparing its vocal output to its memorized template. However, just as monkeys can detect errors and learn to correct them for an external reward of juice, songbird vocal learning can be guided by external factors. A recent study found that spiking activity in Area X neurons was modulated by food rewards and reward signals in an operant task, however the authors concluded the role of Area X in general learning to be “limited and vestigial” (Seki et al., 2014). In contrast, we believe that the contribution of Area X to song learning is vital, and it may be the region that allows external social stimuli to affect song. Area X is highly sensitive to social context, and exhibits a marked, consistent, and rapid-onset response in electrophysiological activity when a female is introduced (Hessler & Doupe, 1999a). Several studies also suggest that Area X is primarily driving song learning rather than production, as the influence of the AFP on motor output is reduced in adults singing stable songs compared to juveniles singing plastic songs (Bottjer et al., 1984; Scharff & Nottebohm, 1991; Sohrabji et al., 1990). Such differing level of activation in different social contexts may reflect a varying level of arousal, or could be specifically related to the communicative function of singing to another bird. In cowbirds, juveniles actively monitor conspecific listeners (West & King, 1988), and it seems probable that zebra finches are doing the same. Area X, via dopaminergic input from VTA neurons, may be responsible for altering the

song in response to social feedback. It may also send song-related information back to VTA via the ventral pallidum, creating a two-way path between socially modulated song learning and reward value. Females have been shown to greatly prefer the song of their mate over the song of other conspecifics (Woolley & Doupe, 2008), suggesting that females are most aroused by song elements similar to those of their mate, resulting in maternal wing strokes that may influence song learning.

In order for rapid social signals to precisely affect the song learning trajectory by targeting specific syllables, Area X would need to receive information on both the precise time in the song at which feedback was received, and the current variability and structure of the song. Area X receives input from HVC in timed bursts which are brief and precisely locked to one time-point in the song with precision on the submillisecond scale (Kozhevnikov & Fee, 2007). This demonstrates that Area X receives a sparse and precise representation of the current time in the song (Fee & Goldberg, 2011), which could be used for Area X to generate a signal to drive variability in LMAN at a specific moment in the song sequence. LMAN also projects indirectly to Area X via axon collaterals in RA, which enables every neuron in LMAN driving vocal variability to be directly “observed” by Area X (Bottjer & Sengelaub, 1989; Vates et al., 1997). Together, this would allow Area X to receive a social reward signal via VTA neurons in response to external feedback, identify the precise time in the song at which the feedback was received, accordingly alter the level of song structure variability at that time-point, and then send this information back to social reward and motivation centers. This hypothesis has never been directly tested, as the role and form of social feedback in zebra finches is only just being discovered, and no mechanisms of socially guided vocal learning have been investigated at the neural level in this species.

## **Conclusions: Social-Motivational Learning in Context**

Behavioral similarities between birdsong and human speech are matched by parallels in the neural system (Bolhuis et al., 2010; Doupe & Kuhl, 1999). Both share a neural dissociation between brain regions involved in the production and learning of vocalizations on the one hand, and in auditory memory and perception on the other (Bolhuis et al., 2012; Gobes & Bolhuis, 2007). Speech and language in humans involves Broca's area and associated regions in the frontal lobe, while perception and memory involve Wernicke's area and temporal lobe areas (Bolhuis et al., 2010). Human language is thought to be dependent on the cortex, however language often develops even in cases of severe cortical damage or complete loss of either the left or right cortical hemisphere (Bates et al., 2001). While catastrophic damage to cortical and sensory systems may leave language unscathed, any alteration to motivational systems proves extremely detrimental (Syal & Finlay, 2011). Until recently, the avian song nuclei were thought to be homologous to mammalian cortical domains (Jarvis et al., 2005), however recent embryological evidence suggests avian vocal areas are limbic (Medina, 2007). As previously discussed, in mammals the limbic areas such as the amygdala and basal forebrain give rise to circuitry involved in social motivation. Placing song learning circuitry regions in areas associated with social reward (Figure 2) opens the possibility that vocal learning is directly coupled with social motivation, and that similar processes may underlie human language learning (Syal & Finlay, 2011).

Virtually all behavioral systems that incorporate learning of any sort are driven by a motivational context. The motivation and social circuits of the brain are inextricably connected, predisposing gregarious organisms to attach reward value to social partners. All that is required for socially guided vocal learning to occur is for evolution to lead to the connection of the social-

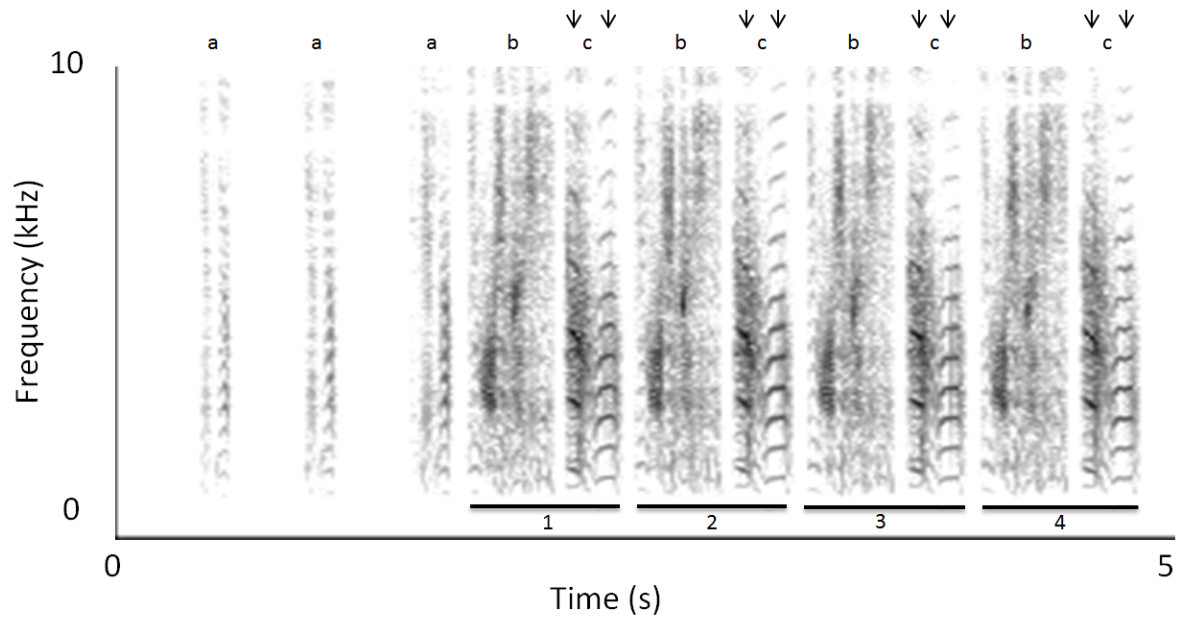
motivation system to the vocal learning system. If song circuitry is indeed homologous to the basal forebrain and amygdala – regions intimately connected to social-motivational circuitry – rather than the neocortex as traditionally presumed, we must use this new perspective to seek homology to songbirds in other vocally learning organisms. Another commonly studied socially guided vocal learner, and potentially equally excellent a model organism for birds as birds are for them, is the human infant. Just as zebra finches can learn from a taped song only when played contingent on their own key pressing (Adret, 1993) and grey parrots fail to learn from non-interactive vocal models (Pepperberg, 1999), human infants are dependent on response contingency to develop mature vocalizations (Goldstein & Schwade, 2008). Infants are sensitive to social contingencies from a young age, and demonstrate varying levels of sensitivity to contingency depending on the general responsiveness of their caregivers (Bigelow & Rochat, 2006).

In species that have evolved socially guided vocal learning, a unique link has been forged between social circuitry and vocal learning systems, such that learning is driven by social motivation. The ‘social gating hypothesis’ was first advanced in work on human infant language acquisition, proposing that language is gated by the motivating properties of social interaction such as attention and arousal (Kuhl, 2007). It has long been known that human parents alter their behavior when interacting with infants, most noticeably changing the prosody of their speech to generate *infant-directed speech*. Compared to adult-directed speech, infant-directed speech is higher in pitch and contains longer pauses, more repetition, and shorter utterances (Fernald et al., 1989), and more effectively attracts and sustains infant attention (Kuhl et al., 2005; Locke, 1993). It was recently found that adult zebra finches alter the structure of their vocalizations when interacting with juveniles in a manner strikingly similar to human infant-directed speech.

When singing to a juvenile, adults lengthen the intervals between motifs, increase goodness of pitch, and repeat more introductory notes before song. Juveniles were also significantly more attentive to this ‘pupil-directed’ song than to undirected song, and those which received a greater proportion of pupil-directed song during development learned better matches to tutor song (Chen et al., 2016). This presents the intriguing possibility that adult finches could be actively teaching song to juveniles, and that, as in human parents and infants, shared attention between tutor and pupil drives vocal learning. Young zebra finches quickly shift the pitch of their song to match that of a movie of an adult tutor facing towards them, but not one facing away from them (Ljubičić et al., 2016). As with zebra finches learning song, human infants learn from caregiver responses which are contingent on their own vocalizations, be they vocal (a tutor song or a spoken word) or non-vocal (a wing stroke or a smile) (Goldstein et al, 2003; Goldstein & Schwade, 2008). Infants also fail to learn the phonemic contrasts of a foreign language unless they are presented by a live, interactive tutor (Kuhl et al., 2003). Learning in both infants and songbirds may be gated by shared attention and social motivation, a process potentially enabled by similar neural circuitry linking vocal learning and social reward.

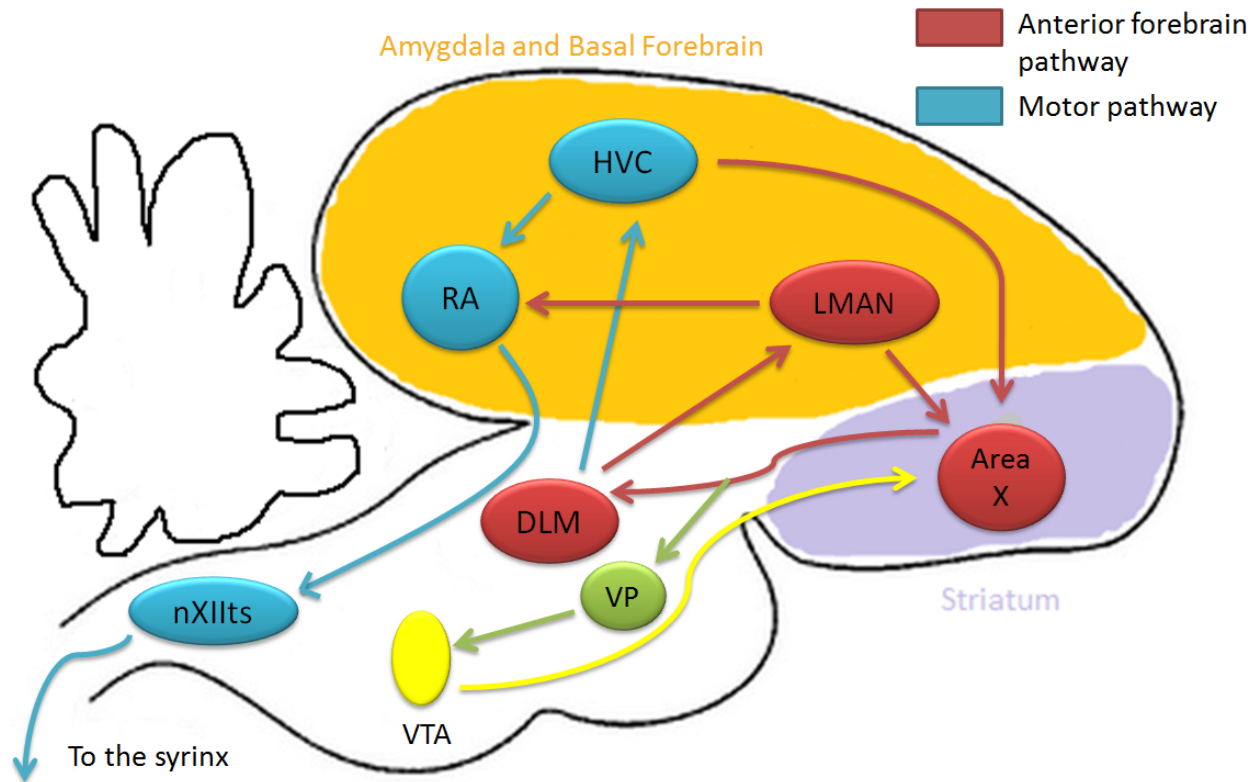
An ecologically valid and more complete understanding of vocal learning requires the incorporation of social factors. Social context and motivation affect the vocal learning system at virtually every level, both behaviorally and neurally. In humans and zebra finches, normal learning fails to occur without social exposure, and moment-to-moment social feedback to immature vocalizations shapes and guides vocal learning. In the songbird brain, social exposure during development leads to growth of HVC, while social context affects activity levels in Area X, which receives dopaminergic input from regions involved in social reward and motivation. Future research efforts should focus on the effects of manipulation of social-motivational

circuitry on social behavior, including sensitivity to social cues, and resulting effects on song learning outcomes.

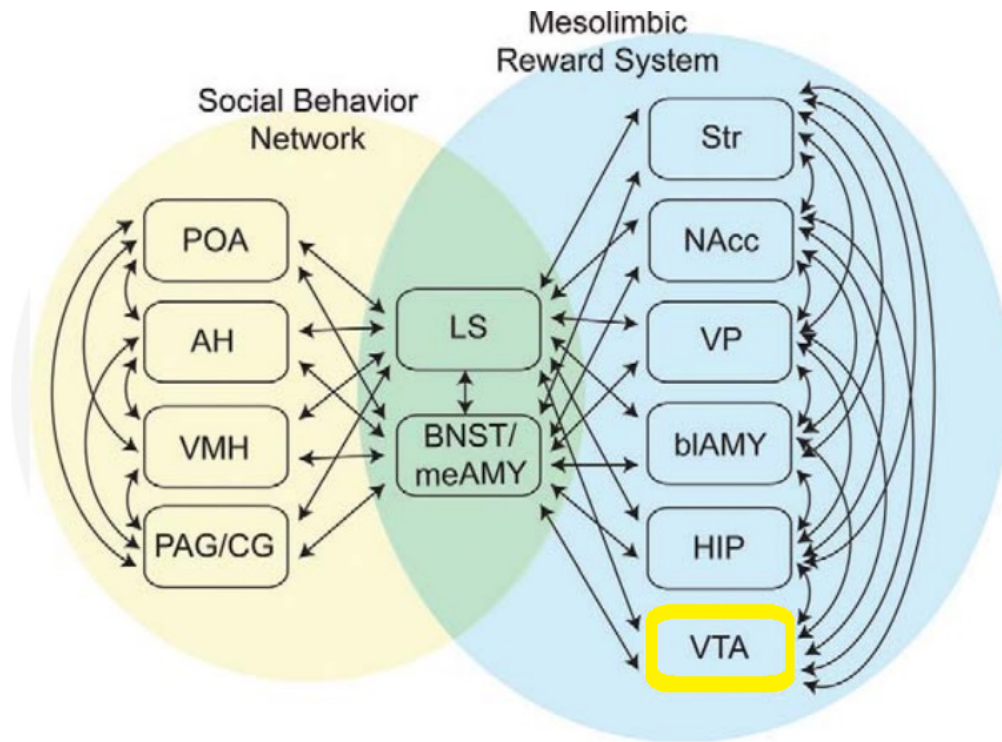


**Figure 1:** Spectrogram of adult zebra finch song with labeled structural components. The song begins with repeated introductory notes ('a') followed by a motif which is repeated several times (bars 1-4). Motifs consist of a number of syllables (identified by letters above the spectrogram). Syllables may contain one or more elements or notes. For example, syllable 'c', which is repeated four times, consists of two notes (denoted by arrows).





**Figure 2:** New thinking on the neural basis for birdsong. The song production pathway (motor pathway) consists of projections from DLM (dorso-lateral division of the medial thalamus) -> HVC -> RA -> nXIIts (indicated with blue arrows). The song learning pathway (anterior forebrain pathway) consists of connections between HVC, LMAN, Area X, DLM and RA (indicated with red arrows). Area X receives dopaminergic projections from VTA (yellow arrow). Area X indirectly projects song-related information back to VTA via the ventral pallidum (VP, green arrows). Based on Syal and Finlay's (2011) concept that brain areas generally believed to be homologous to mammalian pallium (neocortex) more closely resemble amygdala and basal forebrain (in orange) and areas considered homologous to basal ganglia more closely resemble striatum (in purple). This is based on the observation that bird vocal nuclei are located in tissue derived from lateral and ventral pallida, which gives rise to motivational/social circuitry in mammals. HVC; RA, robust nucleus of the arcopallium; LMAN, lateral magnocellular nucleus of the anterior nidopallium; DLM, medial nucleus of the dorsolateral thalamus; VTA, ventral tegmental area; nXIIts, tracheosyringeal portion of the nucleus hypoglossus.



**Figure 3:** Interactive nodes of the networks regulating social decision making, from O’Connell and Hoffmann (2011). Brain regions in the social behavior network (left) and mesolimbic reward center (right) as well as those involved in both systems (center) are shown. VTA has been highlighted yellow to indicate the region by which social/motivational centers project to the song learning system (as seen in Figure 2). Arrows indicate anatomical connections between systems in mammals. AH, anterior hypothalamus; bIAMY, basolateral amygdala; BNST/meAMY, bed nucleus of the stria terminalis/medial amygdala; HIP, hippocampus; LS, lateral septum; NAcc, nucleus accumbens; PAG/CG, periaqueductal gray/central gray; POA, preoptic area; Str, striatum; VMH; ventromedial hypothalamus; VP, ventral pallidum; VTA, ventral tegmental area.

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<sup>1</sup>When housed in acoustic isolation or exposed to passive playback, sedge wrens will improvise song elements, resulting in an approximation of species-typical song.