Social Influences on Song Learning

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Abstract

Social animals must learn during development how to integrate successfully into their group. In vocal learners such as songbirds and humans, the development of vocal communication is initially guided by social interactions with the parents. Later on, vocal development is further shaped through interactions with peers and by attending to the consequences of others interacting. It is difficult to assess, however, how social forces combine to shape the outcomes of vocal development. We first review technical advances that make it possible to track social influences on vocal development in songbirds. We then outline methods for simulating social environments of vocal learning. Such virtual environments would present birds with interactive scenarios in order to directly assess social influences over developmental time scales.

Introduction

In most animal species, only a fraction of juveniles survive to maturity. In addition to being small, inexperienced, and vulnerable, young social animals must also learn how to successfully integrate within their group. They must learn how to identify and interact with friends and enemies [1,2], and how to utilize public and private space [3]. In vocal learners such as songbirds and humans, juveniles must also learn complex vocal communication skills, which are often initially shaped by social interactions with parents. Later, social learning continues not only through direct (potentially agonistic) interactions with peers but also by attending to the consequences of interactions between others (Fig. 1). The complexity of these factors, and the long duration of vocal development, make it difficult to assess how social forces combine to shape the outcomes of vocal development [4].

In humans, even two-day-old infants prefer to listen to infant-directed speech [5], which is higher in pitch, simplified in grammar, and slower overall [6]. These manipulations facilitate word recognition [7] and segmentation [8] by infants. The timing of vocal exchanges with the caregiver is particularly important: nine-month-old infants can quickly match the phonological structure of their mother's vocalizations, but only if she answers their babbling promptly [9].

Similar influences have been observed in songbirds: juvenile zebra finches produce poor imitation of non-interactive song playbacks, but copy live tutors with high accuracy [10,11]. Vocal development in songbirds is also susceptible to complex social interactions with peers and adults other than parents [12,13]. There is a large diversity of song learning strategies across songbird species: there are differences in the timing and speed of learning, repertoire size, and the degree of imitation [14]. Here we focus on songbirds that are age-limited learners, where social influences occur within a narrow developmental window [14,15], making it feasible to track an entire vocal development under controlled conditions [16,17]. We review recent technical advances for quantifying the cumulative influences of social factors on vocal development. We start with techniques for tracking vocal interactions, non-vocal communication, and eavesdropping. We then present a framework for a more ambitious approach of experimenting with virtual social environments (VSE), in order to test the influence of specific social variables and potential synergies between them. If successful, VSEs could test a broad range of hypotheses about how songbirds interpret and incorporate social information during vocal development.

Social influences on vocal development

The social environment can potentially shape the course of vocal development in three ways:

Vocal interactions: The role of auditory input on vocal development is much more extensive than merely providing ‘sensory templates’ for imitation. In humans, turn-taking and overlap avoidance are universal across languages, and minor variations in turn-taking tempo can define cultural identities [18]. At three months old, infants are already attentive to minor temporal delays in interactive episodes with their mothers [19], suggesting that perception of turn-taking rules develops very early. Many animal species, including vocal-non-learners, exhibit antiphonal vocal exchanges. Juvenile marmoset monkeys, for example, learn to avoid call overlap with family members [20*]. It is not known if antiphonal calling affects song development in songbirds, but since juveniles typically exchange thousands of calls with parents and peers every day [21], developmental effects are likely.

Non-vocal communication: Nonverbal maternal responses increase the complexity of an eight-month-old’s speech, but only if these are contingently related [22]. Fourteen-month-olds will turn their head at a pointing gesture, and by 18 months they will use this social cue to learn new words [23]. Non-vocal gestures appear to affect vocal development in songbirds as well, often in subtle ways: female cowbirds, which do not sing, guide juvenile males to produce certain dialects with quick wing strokes or beak gapes [24,25]. Remarkably, lesioning forebrain song nuclei eliminates the female’s preferences for high quality songs and generates disruptions within the social network [26**]. In zebra finches, a large array of both affiliative gestures and aggressive interactions, such as preening and feeding or chasing and pecking, appear to correlate with tutor choice [27,28], but controlling for such social influences is challenging.

Eavesdropping: In order to acquire an appropriate vocal repertoire, juveniles need to learn about their surrounding social network. Human infants as young as 18 months can learn new words from overhearing adult conversation [29]. Until recently, the capacity to make social inferences via observation was thought to exist in only a few species of non-human animals, but it now appears that many species of birds also take advantage of eavesdropping to acquire vital social information. For instance, juvenile song sparrows silently eavesdrop on interactions between adult males [30], and often imitate more songs from an adult they hear interacting with another juvenile than one they interacted with directly [31]. Here, the timing of song learning is

important: adult males only tolerate immature males within their territory, which suggests that opportunities for *direct interactions* may exist during early learning, while limited to *eavesdropping* later on [32]. In a laboratory setting, canaries that overheard overlapping songs between two males were less likely to call to the interrupting “winner” male at a later time [33]. This could mean that they perceive and remember dominance in singing interactions. Finally, cowbird females attend to the calling behavior of other females in their flock, producing more copulation displays in response to male songs previously associated with female calls [34]. These findings, however, have limited bearing on whether juvenile songbirds extract information by observing social interactions and how this affects song development.

Tracking social interactions during song development

Song learning is a means by which an individual establishes its place within a social network. Recent advances in computation power, data storage, and miniaturization of electronic devices have made it possible to study song development continuously [35,36] and even across generations [37], but only in laboratory environments where social interactions are either restricted, or nonexistent. Field studies provide ecological validity, but monitoring vocal development in the wild is usually not feasible. As a result, cultural transmission of birdsong has been studied almost exclusively by sampling mature songs and quantifying population-level vocal changes over time [38,39]. Although it is still prohibitive to study song learning continuously outside of the lab, technologies for tracking individual behavior in social environments are rapidly emerging [40*]. Recently, the spread of new foraging techniques in wild great tits was recently tracked over several weeks, revealing a gradual cultural spread with the emergence of strong conformity to cultural norms [41]. Similar tracking of individuals was used to determine changes in zebra finch social networks due to developmental stress [42] but was limited to identification of birds at feeders and did not track moment-to-moment interactions between individuals within the network. Adopting a similar approach in order to study vocal learning would require continuously recording vocalizations, relative 3D location, heading, and mechanisms for detecting non-vocal gestures:

Tracking vocal interactions: In humans, the LENA system [43] now allows dense sampling of early speech development over several months. Similarly, tracking vocal interactions in small songbirds is now feasible using lightweight wireless microphones [44,45**]. At least in semi-natural aviaries in the lab, these techniques now allow for tracking vocal interactions during pair-bond formation [46] and could be easily extended to juvenile song development [17].

Tracking relative location and heading: In animals where movement is restricted to two-dimensional planes, it is relatively easy to track location and heading of multiple animals in social environments (e.g.: fruit flies [47], mice [48] and fish swimming in shallow waters [49,50*]). GPS has been used to track movement patterns in humans [51] and wild baboons [52], and 3D image analysis has been used to capture aerial displays in starling flocks [53,54]. In insects, tracking 3D trajectories requires highly controlled environments [55]. To our knowledge, no techniques are currently available for monitoring the 3D moment-to-moment movements of small songbirds in a social environment over the course of song development. However, it is likely that combining the above technologies will make this possible soon.

Tracking non-vocal gestures: Recently, several groups have developed techniques for automatically classifying predefined behaviors, such as social interactions in mice [48] and fruit flies [47], and courtship behavior using 3D body postures in mice [56]). There are both technical

and conceptual issues inherent in using automated detection of ethologically meaningful gestures. However, even a crude detection of body postures [56] or gaze [47,54] could be useful for studying social effects on song learning.

Toward virtual social environments (VSEs) for studying vocal development

Continuous monitoring of social interactions is likely to provide deeper understanding of song development. However, establishing causality from such complex longitudinal data is unlikely to succeed unless complemented by controlled studies. We suggest that this can be achieved by developing VSEs that simulate the social context of song learning, through iterative interactions between the developing bird and a computerized visual and vocal interface. Video playbacks have been successfully used to study avian visual communication [58,59], species recognition [60,61], and individual recognition [62,63], though their use in song learning has been limited [64]. Accurate color rendition is a concern because of species differences in color sensitivity [65,66], but some bird species can nevertheless discriminate between individuals on regular computer screens [62,63].

If successful, virtual reality experiments could potentially combine ecological validity with experimental control [67]. One of the most successful virtual environments for studying animal behavior is the *Drosophila* “flight simulator” [68,69]. In these experiments, a fruit fly is suspended, tethered to a tiny rod. As the fly attempts to move, forces generated by its wings feed back to an interface that moves and rotates a surrounding display image in a manner that simulates active navigation flight. Similar approaches were recently used in the mouse [70,71*] and in humans [72]. Once established, such virtual reality scenarios can bypass physical and biological constraints: fundamental questions about spatial learning may be tested by controlling how movement affects perspective in virtual spatial navigation tasks [71]. We propose trying a similar approach to the study of social influences on vocal learning, specifically at the level of direct social interactions, eavesdropping, and statistical learning.

Simulating social interactions: In a VSE, the relative contributions of different sensory information to song learning may be titrated in a controlled manner. In our lab, we are now testing if the orientation of a virtual adult tutor (Fig. 2A) may affect the juvenile’s late-stage developing song. Our preliminary results show that birds quickly shifted pitch to match the song of a virtual male that appeared to be singing towards them (Fig. 2B). We plan to use the data from these non-contingent virtual scenarios to establish a baseline for more complex VSEs, where visual and auditory stimuli are interactive [73].

Simulating eavesdropping scenarios: One of the most exciting questions that VSEs may answer is how, and at what level, a juvenile bird can learn to incorporate observed social information into its song. For example, to what extent can a bird derive social rules from observing aggressive interactions? Suppose that bird A displaces bird B, but bird B displaces bird C: will the juvenile observer infer a linear hierarchy from those pairwise interactions [74], and use this information to alter its developing song? Such an inference could affect moment-to-moment behavior (e.g., deciding which virtual bird to approach or exchange calls with [33]) as well as developmental trajectories related to tutor choice and song convergence or divergence within the peer group.

Simulating statistical learning scenarios: Human infants can perceive statistical regularities in spoken language very early [75], which helps them to segment spoken language into words and

sentences [76]. It is unknown to what extent songbirds acquire and use statistical information in the context of vocal development. At the simplest level, one might ask if social birds can keep track of the individuals around them, and relate this information to their own actions. For example, imagine a VSE where natural variations in song structure become contingent upon dynamic changes in the sex ratio of bird images presented: will the juvenile perceive this contingency and alter its song so as to attract more females (Fig. 3)? If successful, tracking vocal changes this way would reveal which statistical rules are most effective in dynamically inducing vocal changes. Similar approaches could be developed for testing sensitivity to spatial and contextual rules of singing behavior.

Conclusions

A major appeal of studying birdsong is the fact that, like human language, it is culturally transmitted. Figuring out how social processes accumulate to shape vocal learning in songbirds is within reach. In this review we highlighted three categories of social factors that are likely to play a role in vocal development in both humans and songbirds: vocal interactions, non-vocal communication, and eavesdropping as means of acquiring pragmatic information about the social world. We suggest that these factors may modulate sensorimotor learning mechanisms that are well understood in songbirds, through many development studies [77]. Designing VSEs to test specific hypotheses about social influences on vocal learning could provide an inroad into the ecological complexity of vocal development without sacrificing experimental control.

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FIGURE LEGENDS

FIGURE 1. Vocal development may be influenced by many social experiences. These include direct vocal and non-vocal interactions, and observed or overheard interactions between others. At any point in developmental time, these influences can have varying effects as the bird’s social networks increase in complexity.

FIGURE 2. Virtual Social Environments (VSEs) can be used to isolate the effects of specific social and visual variables on song development. In this example we test if songs that are directed at a juvenile are more influential than songs that are not directed toward him. **a)** We first used operant playbacks to train young zebra finches to imitate playbacks of a 3-syllable song (ABC). Once birds had produced recognizable song copies, but before the end of the sensitive period [36], we placed each bird in a virtual social environment where one video displayed a virtual tutor singing towards the pupil, while the other video showed a second virtual tutor, who appeared to be singing away from the pupil. We altered the pitch of one syllable to be either slightly higher (ABC+) in one virtual tutor, or lower (ABC-) in the second one. **b)** Developmental trajectories of two birds show that birds can quickly adopt a song variant based on visual features. Recording the entire vocal behavior of the bird enables us to detect the exact moment where vocal changes occurred [17]. Each line in the plot represents one song motif. Red arrows indicate the onset of VSE training. The pitch of the C syllable is outlined in color. Left: pitch decreases, to match ABC- song of a virtual tutor singing facing the bird. Right: pitch increase, to match ABC+ song of a virtual tutor singing facing the bird.

FIGURE 3. Virtual Social Environments can be designed to test how developing songbirds use statistical rules to guide vocal learning. Here, the VSE changes dynamically via real time pitch detection. As the bird sings, the pitch of his song alters the ratio of virtual females to males facing him, allowing us to test if the bird will perceive this contingency and adjust his song to attract more females.

Figure 1

FIGURES

Figure 2

Figure 3