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Learning in the time of COVID: Insights from the zebra finch – a social vocal-learner

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Introduction

Social deprivation during development has detrimental effects on learning. The COVID-19 pandemic has necessitated social distancing measures including remote instruction for many students, decreasing opportunities for social interactions with teachers and peers. Distanced learning disproportionately affects children of lower socioeconomic status, putting them up to an estimated half-year behind [1]. Meanwhile, children of high socioeconomic status with greater access to in-person learning opportunities and more reliable access to technology are on track to meet usual milestones [2*]. While this inequity cannot be fully remedied by adjustments in remote teaching styles, a better understanding of how to optimize remote learning to be more engaging may mitigate some detrimental effects. For insight to neural mechanisms that can be targeted to improve remote learning we turn to the zebra finch, a social vocal learner and established model species in behavioral neuroscience. Adult male finches sing courtship songs to attract females. These songs are learned during development similar to how infants acquire speech (see Figure 1 for a schematic of vocal learning timelines) [3]. Like humans, zebra finches require social interactions to learn their vocalizations; social deprivation causes song and language deficits [4]. Notably, specific conditions have been identified in which zebra finches can compensate for lack of typical social interactions to develop normal adult song. Here we review recent insights on the underlying neural mechanisms, as well as the influence of neuromodulation due to social interactions.

Imitative learning and the zebra finch

Adult male zebra finches sing complex, stereotyped courtship songs. Juveniles learn songs from an adult male "tutor" via an imitative process consisting of two partially overlapping phases: an initial passive sensory phase during which the tutor's song is obtained as a template, and a sensorimotor period during which the song is practiced and refined before it becomes stereotyped, or 'crystallized', in adulthood (Fig. 1). Mature song consists of bouts which each contain several repeated multi-syllable motifs preceded by one or more introductory notes. The structure of birdsong allows for quantification of similarity to the tutor song at both phonological and sequencing levels and can be interpreted as a proxy for learning. Several well-validated methods for quantifying vocal learning include Song Analysis Pro [5], Vocal Inventory Clustering Engine [6], and other quantitative approaches (e.g. [7]). Recent analysis of overall song structure has additionally identified inter-motif, connective song elements with conserved properties [8]. Emergent machine learning algorithms are being employed to evaluate vocal imitation (e.g. [9*]). These provide insight into specific learning strategies employed by juveniles during different stages of template learning and sensorimotor exploration.

Parallels with human language development

Both babies and fledglings produce unlearned vocalizations required to gain attention from caregivers. In adulthood, both male and female finches produce additional calls used for individual recognition suggesting an extraordinary level of auditory perception [10**]. In zebra finches (but not a majority of songbird species) song learning is sexually dimorphic such that only males learn to produce courtship songs which females judge. The developmental timeline for song learning is analogous to infants acquiring speech (Fig. 1). From 0-6 months, babies passively listen to adults which results in a preference for syllables specific to the language of their caregivers. This reflects emergent tuning of the auditory cortex towards language-specific sounds, analogous to how changes in auditory cortex responsiveness to conspecific song emerges during the sensory phase in juvenile finches [11*]. After 6 months, infants begin babbling and gradually produce specific words and phrases via sensorimotor trial-and-error learning. Similarly, songbirds enter a sensorimotor critical period in which they use auditory feedback of their own vocalizations to gradually produce a match to the stored tutor template [12].

Effect of social deprivation

Lack of exposure to adult speech during development has devastating consequences emphasized by the Bucharest Early Intervention Project in which Romanian orphans who had been severely neglected were placed in a randomized, controlled trial looking at the effects of foster care on general well-being [13]. The younger the child received the intervention, the better the improvement in language ability, reinforcing the presence of a sensitive period for language development. Similarly, better verbal outcomes are seen in deaf children who receive cochlear implants earlier in development rather than later [14]. As a caveat to what follows, many school-age children affected by COVID-19 shutdowns are beyond the sensitive period for language acquisition but are still within a sensitive period for sensorimotor learning of various skills. This presents a special concern for children with mild to moderate neurodevelopmental or learning disorders who may experience a delay in receiving proper diagnosis and treatment. Research on critical periods in zebra finches reveals insights about the specific effects of social deprivation on behavior and how these may be mitigated.

Deficits in song complexity

In addition to the complex structure of song bouts, characteristics such as pitch and entropy of individual syllables are faithfully duplicated from the tutor template. Birds raised without a tutor or that are deafened prior to the critical periods sing simple songs that consist of fewer and longer syllables, incorporate unlearned notes often with a high degree of frequency modulation and lack a true motif-like structure [15]. In female preference tests, these so-called ‘isolate’ songs prove unattractive [16*].

Critical period extension

While the absence of social tutoring has detrimental effects on song development, a mark of resilience is that songbird isolates experience a brief extension of their critical periods whereby they can successfully obtain a song template when a typically reared bird (Fig. 1). This short-term effect allows the juvenile one last chance to acquire a template [17]. The sensorimotor critical period can also be extended through auditory interference [18]. These findings suggest that the nervous system has evolved to retain plasticity before ‘closing the door’. Indeed, both humans and songbirds exhibit neoteny meaning that they are born or hatched at an early developmental stage, enabling environmental exposure to shape and fine-tune neural circuitry [19]. One goal of learning in the time of COVID is to identify therapies that extend critical periods, reopen them and/or speed up behavioral remediation [20*].

Sparse exposure to tutor song is still effective

Juveniles can fully obtain a song template with sparse exposure to the tutor: Only one short session with a tutor in an otherwise isolated juvenile results in a song that is much more appealing to females. Five sessions result in a song indistinguishable from non-isolated birds [21*]. Interestingly, juveniles pay more attention to adult males who sing fewer motifs around them. Thus, over-exposure to the tutor song leads to poorer learning. Here the lesson for remote learning is to pay attention to findings from educational research which demonstrate the beneficial effects of spaced learning epochs, as well as timing these epochs to the optimal circadian rhythms of the pupil [22]. Juvenile zebra finches within the sensorimotor critical period sing in spaced bouts of intense practice and rest; deviations from this spaced epoch pattern result in poorer learning [23]. Additionally, proper sleep between learning bouts plays an important role in language learning in both finches and humans, with poor or insufficient sleep associated with suboptimal learning outcomes [24, 25]. While the optimal amount of sleep for children varies with age, sleep researchers have largely taken the position that school starts too early in the morning, particularly for adolescents, resulting in chronic sleep deprivation and associated poor academic performance; pushing back school start times would have broadly beneficial effects on learning and health [26]. Rather than a disadvantage, virtual classrooms can enable these features through asynchronous learning activities [27*].

Social isolates can learn from a taped song under operant conditioning

Early studies suggested that isolated juvenile finches could not successfully acquire a song template from an audio recording of adult song. Similarly, simply taping and uploading old lectures and delivering them virtually to students in a passive format fails to engage remote learning. Subsequently, it has been shown that isolates learn well from a tape recording if they must peck a key (or pull a string) in order to trigger a song playback [28]. Presumably, placing playback under operant control taps internal reward mechanisms that facilitate learning. This suggests that in the absence of live tutors, "gamifying" learning can be effective [29, 30*]. An example in humans is the language-learning app 'Duolingo' which incentivizes daily practice intervals with a number of measures including keeping track of multi-day streaks and overall learning goals and providing near-instant feedback with a chime that plays for each correct answer. This operant feedback likely boosts the endogenous reward aspects of learning. Additional work in Bengalese finches indicates that optimizing instruction for an individual's genetic background also boosts learning [31**]. An extension to humans may be to provide a set of diverse instructors so that students with individual differences in learning styles have more opportunities for engagement [32, 33]. Interestingly, aspects of gamification that entail inter-student competition are not as effective [34].

For male zebra finches, song is rewarding in part because it is linked to successful reproduction by serving as a signal of fitness to females [16*]. However, mature song must be obtained via extensive sensorimotor learning well before the extrinsic reward of a female is present. What motivates young males to practice their songs prior to the rewarding opportunity to mate? Remarkably, undirected song, which can be thought of as practice, is intrinsically rewarding to juveniles by triggering dopamine release within the striatum [35**, 36**]. The sensorimotor stage of song learning may thus be considered a type of play, an evolutionarily conserved behavior [37**], which can develop motor skills in juveniles and provide intrinsic reward via neuromodulatory mechanisms (see below). A goal of remote learning in humans is to capitalize on such intrinsic mechanisms to make individual and asynchronous work more rewarding.

Learning substrates in the song control system

Motor control of song

The song control system consists of the motor pathway necessary for singing, and the anterior forebrain pathway (AFP), necessary for song to change, e.g. during learning [38]. The motor pathway comprises the robust nucleus of the arcopallium (RA), the primary motor cortical region dedicated to song and analogous to laryngeal motor cortex in humans [39; 40]. RA receives excitatory input from the premotor nucleus HVC (proper name). Inputs from higher level auditory areas first enter the song control circuit at HVC making it a nexus for sensorimotor integration. Indeed, HVC neurons exhibit both sensory and motor activity. Their activity provides sparse coding for motor output [41] but they also fire in response to hearing their own songs or those that resemble them [42] thereby exhibiting mirror neuron-like properties [43]. In addition to this motor pathway, HVC neurons participate in the anterior forebrain pathway (AFP) made up of striatopallidal Area X (proper name), the dorsomedial thalamus and the cortical lateral magnocellular nucleus of the anterior nidopallium (LMAN). The AFP comprises a cortico-basal ganglia loop similar to those that facilitate the organization of motor programs in vertebrates. These two circuits are interconnected, most notably in songbirds via HVC inputs to Area X and via LMAN inputs to RA.

Translational significance

The zebra finch song system shares a striking degree of similarity to human brain regions involved in speech despite the evolutionary distance between the two species. Transcription profiles in song-related regions of the zebra finch brain more closely resemble those in analogous regions of the human brain compared to non-vocal learning birds [39]. Specifically, human laryngeal motor cortex shares a transcriptional profile reminiscent of HVC whereas the human striatum resembles Area X. Recent anatomical studies further indicate that the avian forebrain shares a mammalian cortical-like microstructure [44*]. These similarities extend to neuromodulation: For example, within the basal ganglia, when male finches sing to females (directed song), dopamine levels in striatal Area X are higher than when he practices his song alone (undirected song) [45, 46]. Finally, both songbirds and primates have cortical neurons with mirror-like properties [42, 43]. This remarkable convergence suggests that mechanisms that facilitate or compensate for impoverished learning environments in birds may be tapped for improving remote learning in humans.

Premotor influences

Auditory and mesolimbic inputs mediate song template acquisition

HVC is a premotor output nucleus with mirror neuron properties that depend on higher order auditory inputs. The largest auditory area that projects to HVC, nucleus interfacialis (NIf), is necessary for obtaining the tutor template during the sensory learning phase. Optogenetic activation of this pathway can override acquisition of a normal song [47**]. Specifically, depending on the stimulation protocol, activation of NIf afferents to HVC as a proxy for the tutor song template can instantiate atypically long or short song syllables in the pupil. Presumably, this pathway taps mirror neurons that are endogenously active during the sensory phase when the tutor song helps to encode a long-term template. Social deprivation also impacts tutor song acquisition. Another auditory input to HVC acquires specific firing patterns during the normal sensory critical period. When juveniles are reared without a tutor, these patterns are disrupted [48*]. While impoverished environments lead to learning deficits and neurons with altered excitability, the opposite is also relevant in that enriched environments can enhance motor skill learning and neuronal excitability [49*]. Identification of social and ontological conditions under which sensory inputs are recruited to guide motor output highlights opportunities for augmenting sensory stimuli during remote learning sessions.

Non-imitative social learning

As noted above, undirected singing can be likened to play and recruits endogenous reward mechanisms [35**]. In addition, juveniles receive feedback from adult females during early stages of vocal motor exploration which guides them towards producing more mature vocalizations [50*]. The imitative learning process by which the juvenile bird compares its subsong to the mature song template is thus supplemented by external social feedback. Early immature vocalizations may serve the dual purpose of providing direct sensorimotor information to the developing brain circuits and also engage the caregiver's attention leading to additional opportunities to be exposed to a template and/or gain direct behavioral feedback [51].The challenge for remote learning is thus to recruit the interplay between endogenous and exogenous reward mechanisms. This can entail providing opportunities for students to receive external reinforcement from peers (e.g. via break-out rooms on Zoom©) and instructors (e.g. via polls, remote office hours) as well as providing opportunities for internal reinforcement by offering leadership roles such as 'reporter' and 'scribe' and encouraging the development of supportive internal dialogs.

Optimal song learning requires behavioral variability

Social context affects the precision of song at both the level of neuronal activity within song control circuitry and in the stereotypy of the behavior. As noted above, undirected song practice is more variable and associated with burst firing in the AFP whereas songs directed to a female are more precise and associated with more time-locked activity. In humans, sometimes an audience can bring out the best in a performer; yet other times an audience can be intimidating. Interestingly, in zebra finches, increased song variability during the sensorimotor learning improves adult song as measured by similarity to the tutor template and overall appeal to females. As elements of a song are learned, there is a balance between conserving already well-learned elements while injecting variability towards syllables that require further refinement. Time-locked cortical inhibition during well-learned syllables or song segments allows those elements to be preserved while other syllables are subjected to instability [52*].

New statistical analysis of neuronal activity patterns in the AFP indicates that noisy neuronal bursting during undirected song carries more information than time-locked firing during directed song [53**]. Perhaps counter-intuitively, such 'noise' provides an optimal background for detecting coherent signals (e.g. [54*]). These observations support the value of engaging students in both performance and practice during remote learning by providing opportunities for each. Performance roles such as students recording themselves presenting a project, then iteratively watching themselves, improving their presentations and re-recording may strongly engage the mirror neuron system. Similarly, birdsong research indicates distinct advantages to observational versus experiential learning [55**]. Whereas the former is more rapidly acquired, the latter is more robust and generalizable to new situations. These findings reinforce the pedagogical adage that 'less is more' by shifting the focus from rote memorization to in-depth training on one topic and then offering opportunities to apply that learning to other problems. Anecdotally, remote learning may enhance the engagement of non-dominant personalities by leveling the playing field for participation (assuming equal access to technology; see below) and offering more direct access to instructors.

Endogenous reward mechanisms

Dopamine

The zebra finch brain differentially expresses dopamine receptors in the song control system compared to surrounding tissues, indicating that dopamine is a major modulator including of social contexts [56, 57]. As noted above, Area X dopamine levels are higher when adult males sing to potential mates than when they practice their songs alone. Dopamine release in Area X provides a reward prediction error signal that correlates with song quality [58**]; a reward prediction error signal is also sent from the ventral pallidum to the ventral tegmental area [36**].

In addition to the striatum, a dopaminergic projection to premotor mirror neurons in HVC from the periaqueductal grey is involved in encoding the song template learned from the tutor [59**]. Returning to the issue of live versus recorded training, fascinatingly, this pathway is endogenously active in the presence of a live tutor song, but not in response to a taped recording. This pathway presumably works in concert with HVC afferents from NIf. As noted above, this NIf-HVC connection can be experimentally manipulated during the sensory critical period with optogenetic stimulation to override a juvenile bird's innate preference for a live tutor song [47**]. Further investigation of whether this pathway is active during the operant conditioning paradigm may give insight into whether social and operant reward circuitry is segregated or overlapping.

Nonapeptides

Nonapeptides strongly modulate social behaviors; this family of neuropeptides in mammals includes oxytocin and vasopressin. In avian brains, close analogues arginine vasotocin (AVT) and arginine vasopressin promote organization of social circuits during development and modulate a broad range of social and parental behaviors [60]. During the sensorimotor phase of song development, increases in AVT are associated with increased learning, and blockage of AVT receptors impairs learning. AVT has been proposed to act in combination with the dopamine system [61]; dopamine-expressing ventral tegmental area neurons that send their axons to the striatum express oxytocin receptors on their dendrites and cell bodies. Thus, oxytocin release may modulate dopaminergic release within the striatum.

Opioids and cannabinoids

As mentioned above, natural reward systems are theorized to be involved in crucial play-like behaviors to support the development of necessary motor skills. Endogenous opioids and cannabinoids may play a role in generating the rewarding properties associated with these play-like behaviors. Blocking mu opioid receptors of zebra finches within Area X modulates acoustic properties of song but not the amount of singing, and increases dopamine release, suggesting a close interplay of the dopamine and endogenous opioid systems [62*]. Daily cannabinoid exposure during sensory acquisition affects encoding of the tutor template [63]. Similar exposure during the sensorimotor critical period affects juvenile song development but does not alter song production in adults [64]; effects likely mediated through activation of type 1 cannabinoid receptors [65]. While these findings indicate that normal endocannabinoid signaling plays a role in learning of complex sensorimotor skill, they also highlight similar vulnerabilities of juvenile avian and adolescent human brains to non-physiological levels of exogenous cannabis [66].

What this research suggests about virtual learning during the time of Covid-19

This overview emphasizes the broad importance of social interactions during development on learning and indicates that a return to in-person schooling should be a high priority for reopening. Obviously, there is a limit to what we can glean about education from studying birdsong. The approaches discussed above are likely most applicable to subjects involved in a sensorimotor learning, such as language coursework or study of a musical instrument, rather than those that require memorization of declarative facts. With that said, at least within the US, the current K-12 in person education is not especially engaging for many students. Contemporary cultural depictions of school generally focus on the boredom, tedium, and grind of busywork, with large classrooms and lecture-style teaching. With the logistical adjustments that have to be made for COVID-19 comes an opportunity to revamp the education system by changing the format to emphasize learning methods that engage natural reward mechanisms [67*]. A major goal is to transition juvenile intrinsic reward systems for ‘play’ into targeted neurological mechanisms for behavioral and/or therapeutic enhancement. Possibilities are to enhance the participation of the mirror neuron system through enhanced use of physical gestures and/or audio components and peer interactions, to “gamify” individual work [30*] and to pay attention to transitions in reward mechanisms across development [68*]. These broad approaches harness natural reward mechanisms within the brain, enhancing attention and learning. Another approach will be to focus on targeted remedial measures for the children most adversely affected, by decreasing class sizes and increasing funding for educational enrichment programs.

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