



Editorial



1. Introduction

Songbirds, parrots and hummingbirds learn their vocalizations from adults, similar to how human infants acquire speech. There are interspecies differences in when birds can learn new songs, what kind of songs they will sing, and how large their song repertoires are. All vocally learning birds however, go through a stage of plasticity, a 'sensitive phase', in which an interaction between sensory memory and sensory-motor integration leads to the final production of the learned song.

Song production is controlled by networks of dedicated brain regions, i.e. regions that are specifically involved in song (Wilbrecht and Nottebohm, 2003). These brain regions show many functional similarities to human brain regions that are important for speech (Bolhuis et al., 2010).

The beauty of the avian vocal learner as a model for vocal development lies in the many applications it can harness. For example, avian research can reveal the dynamics between experience-dependent and biological factors, the time course of sensitivities during different stages, or neural markers for development and plasticity. There are diverse applications for avian vocal learning research, for example to study developmental, social, neural, genetic and evolutionary aspects of learned behaviour.

With this Special Issue, we aim to highlight new research directions in birdsong learning. Contributions include a variety of approaches: literature reviews and reports of new data, a range of different bird species, and different research methodologies. Articles in this Special Issue discuss the roles of developmental experience, biological maturation, song model type and availability, and social interaction on birdsong learning, including underlying neural, physiological and (epi) genetic mechanisms.

2. The sensitive phase

The sensitive period for vocal learning in zebra finches has been well described before, but this was often in a single tutor setting, which may not be representative for the natural situation in which birds hear many more individuals. Indeed, when housed in large social groups, juvenile zebra finches often incorporated syllables from multiple adult males in addition to their father's syllables (Williams, 1990). Previous studies show that in single tutor situations, juveniles can memorize and imitate tutor song heard only between 25–35 days post hatch (dph) as well as in an unlimited tutoring setting (e.g., Immelmann, 1969; Roper and Zann, 2006). However, the sensitive phase stays open beyond 35 dph.

Here, Gobes et al. (Gobes et al., 2019) review what is known about the timing of the sensitive phase for song learning in zebra finches and

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provide new data. They use an approach of limited exposure to one tutor, followed by another tutor later in time, to reveal if birds can still learn after the initial sufficient learning period and how much exposure is necessary to override earlier memories. They confirm that zebra finches are still able to learn song from a second tutor up to 65 dph, with 10 days of tutoring between 55–65 dph being sufficient to override song similarity with the first tutor. Tutoring for 5 days only was sufficient at 44–45 dph but not anymore between 68–73 dph, demarking the end of the sensitive phase for vocal learning. This is much later than the minimal required time birds need to learn the tutor song (until 35 dph). Thinking about the time between day 35 and day 65 is relevant for our full understanding of the developmental path of zebra finch vocal learning and neurobehavioural plasticity. The method presented here can be used to study when birds are sensitive to specific features in the signal, to social cues and how brain plasticity changes over the course of development.

London (London, 2019) describes the current state of the rapidly growing field of genetic, molecular and epigenetic mechanisms of the sensitive phase for song learning in zebra finches. She reviews our understanding of mechanisms that promote zebra finch song learning in the sensory acquisition phase, and limit learning at the end of the sensitive phase for auditory learning. She includes her own recent findings that show that the mTOR pathway is of crucial importance for successful song learning at the onset of the sensitive phase. Several potential drivers for the onset and offset dynamics of neural plasticity are described and several lines for future research are proposed. For example, specific genomic manipulations could reveal the mechanisms for onset and offset of the sensitive phase for vocal learning. Moreover, the interaction between age and experience during development can be revealed.

3. Sensory and motor selectivity during development

Within the sensitive phase for learning, several substages have been identified in which specific parts of the learning process take place. In addition to different stages of vocal motor plasticity, birdsong development is characterized by different stages in sensory selectivity. It is becoming more and more clear that birdsong is a combination of predispositions and experience, which both influence neural and behavioural selectivity. The balance between the two, the timing of stages, and the features for which birds are sensitive may differ among species, sex and potentially even individuals within species.

Soha (Soha, 2019) addresses the topic of timing of selectivity in her study on Nutall's white-crowned sparrows. She disentangles selective memorization early in development from selection by attrition during rehearsal later in development. After tutoring with single-phrase songs, she follows the production learning process at multiples stages. She

shows that from the start of song rehearsal, there is a production bias for whistles, but not for conspecific phrases, in contrast to earlier found auditory preferences. Selective memorization of whistles *before* song production possibly leads to an early production bias. Syntactic information (song starting with a whistle) and overproduction (singing more phrases in early than crystallized song) on the other hand, change over the course of development, indicative of a process of selection during rehearsal. Overproduction and whistle bias are experience-independent as this information is not present in the song input, whereas shorter phrases could be influenced by the single phrase tutor-songs.

Riters et al. (Riters et al., 2019) also describe song rehearsal during the developmental stage for song motor plasticity, but with the perspective of vocal “play”. They describe play as a behaviour that is intrinsically motivating, and thereby song “play” may be a driving force for young and adult birds to continue singing outside social, territory or mating context (see further discussion of this article below). Potentially, song “play” could also facilitate learning of specific phrases, if those phrases would be more intrinsically motivating to sing than other phrases. Extrapolating this hypothesis, intrinsic motivation could also guide the song selection process described by Soha, potentially explaining *how* predispositions could affect learning.

Neural selectivity changes over development as well, depending on the age measured (Lampen et al., 2019), the type of early song experience (Diez et al., 2019) and the social context in which auditory stimuli are presented (Yanagihara and Yazaki-Sugiyama, 2019, further discussed below).

4. Early song experience for learning

Social interactions with the tutor are important for song learning (e.g. Chen et al., 2016; Derégnaucourt, 2011; ten Cate and Houx, 1998). Yanagihara & Yazaki-Sugiyama find that neural responsiveness and selectivity in a higher-order auditory brain region during song development are specifically affected by the presence of the tutor. Tutor-song selective neurons responded stronger to tutor song when the tutor was present than to song playbacks alone (i.e. without the presence of the tutor). Furthermore, neurons that were tutor-selective in isolation, became less selective after tutor introduction, as they also fired in response to other sounds. Such enhancement could indicate facilitation of learning by visual or social cues.

Diez et al. (Diez et al., 2019) show that neural responsiveness to songs in auditory brain areas is different between birds with different tutor song experiences early in life. They investigate neurobehavioural selectivity in female zebra finches. Using a variety of stimuli, they identified auditory selectivity and the effect on later neural responsiveness to song playbacks. One of the stimuli used was ‘isolate song’, produced by untutored males, which deviates from the average acoustic space of normal ‘wild type’ song (Fehér et al., 2009). They find different neural responsiveness in adulthood in females tutored with isolate song compared to females tutored with heterospecific or wild type song (using white noise playback as reference). Thus, early auditory experiences shape how the adult brain responds to sound, at least in females.

Taken together, the above studies highlight that auditory perception, production, brain maturation, experience, social context and intrinsic reward all interact in shaping brain and behaviour. Especially the developmental timing of internal mechanisms and experience is relevant for all the above findings.

5. Song rhythmicity

Zebra finch song has a regular rhythm (notes in a fixed sequence that are repeated: e.g., ‘ABCD ABCD ABCD’). The silence durations between syllables are very stereotyped across song repetitions – though slightly less so than the extremely precise syllable durations (Glaze and Troyer, 2007). Lampen et al. (Lampen et al., 2014) made irregular song

stimuli by altering inter-syllable interval durations in natural song. With these stimuli, they previously showed in adult male and female zebra finches that more neurons in auditory brain regions were active in response to irregular than natural song. This could be explained by a “novelty (or mismatch) response” in the auditory areas: the detection of an unexpected deviation of the learned song rhythm leading to stronger neural responses. Here, Lampen et al. went on and tested neural responses to the regular and irregular stimuli in juveniles. In contrast to adults, higher-order auditory activation levels were similar in response to regular and irregular song in 6 weeks-old juveniles, suggesting that more learning or exposure is needed for developing the novelty response. However, in 4 weeks-old juveniles, there was an increased response to the irregular song stimulus in one of the higher-order auditory brain regions. The authors link this result to the learning stage that birds of this age are in (the template acquisition stage). The discrepancy between 4 and 6 weeks-olds could indicate there is an early ‘innate’ bias for natural rhythmicity of song, which is later affected by experience-dependent changes in neural responses during song learning, but needs more time to fully develop. Future research may help to discover more about the developmental trajectory.

When a bird sings the same motif several times in a row (e.g., ‘ABCD ABCD ABCD’), the rhythm of song would be regular. However, Hyland Bruno & Tchernichovski in this issue (Hyland Bruno and Tchernichovski, 2019) show that there is more complexity to how zebra finches compose song bouts, where birds flexibly inserted connector syllables between motifs (e.g., ‘iii ABCD i ABCD ii ABCD’), generating a less regular rhythm. The authors suggest that sequence variability at the bout level could allow birds to use song to communicate about behavioural states, even in species that sing only a single stereotyped motif (‘ABCD’), such as the zebra finch

Controlling the precise timing of song perception and production is even more pronounced in duetting birds (Rivera-Cáceres and Templeton, 2019; see further discussion below). Duetting bird pairs sing songs in precise coordination with each other, and use temporal cues in each other’s song for predicting how to proceed.

Together, these studies show that temporal information is relevant in both perception and production. However, selectivity for specific auditory features may differ with age and/or experience and sex and species. Longitudinal studies could shed light on these issues.

6. Females and song

The classic male-female comparison in birdsong research is focussed on song in males versus no song in females. As Perkes et al. (Perkes et al., 2019) point out, in many species of songbirds, especially those that live in tropical rather than temperate areas, both male and female songbirds learn to sing (Odom et al., 2014). In those species, the two sexes have similar neural and biophysical mechanisms for song. However, in some songbirds, such as the often-studied zebra finch, or the cowbird, only male birds sing and females do not. Females often prefer specific variants of male songs, such as long, complex song sequences. Perkes et al. in this issue describe the neural mechanisms of song selection in the broader sense in females. In non-singing females, mid-brain regions, song system nuclei and auditory regions are important for song evaluation, courtship behaviour, and control of the timing of production of non-learned vocalizations (“calls”).

Rivera-Cáceres and Templeton (Rivera-Cáceres and Templeton, 2019) review the ontogeny of duetting. Two aspects specific to duetting species are highlighted: the ‘rules’ or duet codes and precise timing of interaction and sex-specific repertoires. Probably, some of the code is learned early in ontogeny, but since the duets are only used later in life when forming a new pair with different song, new codes have to be learned in adulthood. How juveniles learn their sex-specific repertoires is not yet clear. The authors suggest sex-specific song structure is likely learned early in ontogeny and social interaction with the tutors is crucial. Suggested new lines of research will have to reveal if females

have different developmental timing than males, a different template and/or if social interactions can explain sex-specific repertoires. Research in both field and laboratory experiments are necessary and comparison with other avian vocal learners and non-learners could reveal more about duetting mechanisms, which help us understand vocal learning mechanisms in general.

Similar to other species of songbirds such as zebra finches, Tobin et al. (Tobin et al., 2019) show here that there is a difference in song directed to different audiences in budgerigars. Warble songs directed to females had more consistent element ordering compared to warbles sung to males. Interestingly, this was true across birds: males had similar ordering rules for warble element types, and those rules were more consistent across males when singing towards females. Other aspects of the warbles, such as total warble song duration or proportions of specific song elements, did not differ between audiences. The authors discuss why female-directed warbles may have more consistent song sequences - it could be that females prefer more consistent songs, or consistent songs may be more effective at stimulating females' reproductive behaviours. Literature suggests that male-directed warbles promote breeding synchrony across pairs.

7. Reward-systems in the brain

Birdsong is thought to be important for the functions of territorial defence and mate attraction. However, birds sing ubiquitously outside of these contexts. For example, birds typically sing at high rates when they are kept in social isolation. Such singing outside of functional contexts may be considered as a form of play. One important aspect of play behaviour is that it leads to a more positive affective state, i.e. it is rewarding to the animal. Ritters et al. (Ritters et al., 2019) discuss the evidence showing that singing is indeed an intrinsically rewarding behaviour. The authors discuss evidence that birdsong in not fully functional contexts also stimulate neural mechanisms that promote a positive affective state, including opioid and endocannabinoid neuromodulators and the mesolimbic brain pathway. Thereby they show that songbird brain mechanisms for non-sexual and non-territorial singing are analogous to those involved in mammalian play.

8. Birdsong & speech

The study of birdsong and other avian vocal learners is often used to help understand mechanisms that also underlie human speech. Parallels have been suggested for development, neural processing and control, auditory-motor interaction, genetic and possibly hormones. Several articles in this Special Issue add novel similarities to these known avian-human parallels, and known similarities are investigated in more detail.

Gobes et al. (Gobes et al., 2019) show plasticity during development later than previously thought but not unlimited, which they (carefully) compare to human second language learning. Even though there are still clear differences between speech and birdsong, possibly the mechanisms of closing and ending sensitive phases likely show parallels. When children learn a second language during for example puberty, they have already learned all language components on their first language, but are still capable of acquiring a second language 'native-like' (Johnson and Newport, 1989)

Rivera-Cáceres & Templeton (Rivera-Cáceres and Templeton, 2019) draw a relatively novel parallel between turn-taking in human speech and song: duetting. The authors suggest that during vocal learning, also the duetting or turn-taking rules may be learned. Moreover, both males and females take part in duetting song, as well as in human turn-taking.

Lampen et al. (Lampen et al., 2019) compare avian and human rhythm perception. In humans, rhythmicity in speech may be a relevant cue for infants to learn and segment speech into units (Johnson and Seidl, 2009). It is still an open question to what extent birds segment vocalizations into separate units, and how acoustic cues can help them

do this (Mol et al., 2016). The work by Lampen et al. suggests that birds are, at the very least, sensitive to temporal information in the signal.

Pike & Kriengwatana (Pike and Kriengwatana, 2019) describe perceptual mechanisms that deal with variation in (vocal) signals that can potentially disturb signal transmission, and with that the information encoded in the signal. In humans a mechanism called "vocal tract normalization" makes it possible for us to understand speech produced by different speakers and in different situations, despite these disturbances. Pike & Kriengwatana elaborately review the similarities and differences between avian vocal learners and humans in terms of vocal tract variation and dealing with this variation perceptually. They suggest that there is enough variation to think that birds need some sort of normalization. However, relatively little is known about how birds do this, and it is also unknown if it is unique for vocal learners or general across other (non-vocal learning) species. The authors present several relevant new lines of research to answer these questions.

9. Individuality in vocal production and perception

Birds can recognize others based on song alone (e.g., Miller, 1979). One of the questions raised by Pike & Kriengwatana is how individual recognition is affected by signal transmission quality or other variable factors. One of such factors might be stress, as stress affects for example the call frequency and amplitude (Perez et al., 2012).

Soula et al. (Soula et al., 2019) study whether stress induced variability in individual vocal production can disturb communication. They use machine learning techniques to predict which type of information in the signal can potentially be used to discriminate between individuals despite stress induced variation. They trained learning algorithms on a subset of calls to classify calls either by individual or by 'emotional state' (stressed/unstressed). The algorithm performed best on individual recognition if the training subset included both emotional states. However, even if it was trained with only one emotional state, performance dropped but was still above chance. When the algorithm was tested on classifying emotional state and only a subset of individuals was used for training, performance dropped to approximately chance level. Together, their results indicate that based on acoustic features there is an influence of stress and familiarity on learning performance of the algorithm, but despite variation due to stress, individual recognition by the algorithm is not completely lost. Whether or not real zebra finches would discriminate calls in a similar way remains to be tested, but the machine learning method provided allows researchers to more efficiently select hypotheses before testing animals, which has advantages in both ethical and efficiency reasons. We expect that this method will be used more frequently in the near future and will help make research more efficient.

In relation to speech research, the above findings are also relevant given the parallel between individual recognition and speech register described by Pike and Kriengwatana. Potentially, the algorithm performs a 'normalization' similar to what humans and possibly songbirds do.

10. Concluding remarks

There is a rich foundation of knowledge from earlier years in the avian song learning field, from which we have learned not only how birds learn to sing, but also to understand some of the mechanisms that underlie speech acquisition in human infants. In this Special Issue, several exciting novel avenues are included that will likely be explored more in the near future, such as interacting factors during development. New methodologies will help make progress and address questions that could not be answered before, such as state-of-the-art techniques in neuroscience, genetics, live-tracking of animal behaviour, or bioinformatics. The collection of recent findings in avian song learning in this Special Issue highlights there is a strong future ahead for the study of avian song learning.

References

- Bolhuis, J.J., Okanoya, K., Scharff, C., 2010. Twitter evolution: converging mechanisms in birdsong and human speech. *Nat. Rev. Neurosci.* 11, 747–759. <https://doi.org/10.1038/nrn2931>.
- Chen, Y., Matheson, L.E., Sakata, J.T., 2016. Mechanisms underlying the social enhancement of vocal learning in songbirds. *Proc. Natl. Acad. Sci.* 113, 6641–6646. <https://doi.org/10.1073/pnas.1522306113>.
- Derégnaucourt, S., 2011. Birdsong learning in the laboratory, with especial reference to the song of the Zebra Finch (*Taeniopygia guttata*). *Interact. Stud.* 12, 324–350. <https://doi.org/10.1075/is.12.2.07der>.
- Diez, A., Cui, A., MacDougall-Shackleton, S.A., 2019. The neural response of female zebra finches (*Taeniopygia guttata*) to conspecific, heterospecific, and isolate song depends on early-life song exposure. *Behav. Processes.* <https://doi.org/10.1016/j.beproc.2017.12.022>.
- Fehér, O., Wang, H., Saar, S., Mitra, P.P., Tchernichovski, O., 2009. De novo establishment of wild-type song culture in the zebra finch. *Nature* 459, 564–568. <https://doi.org/10.1038/nature07994>.
- Glaze, C.M., Troyer, T.W., 2007. Behavioral measurements of a temporally precise motor code for birdsong. *J. Neurosci.* 27, 7631–7639. <https://doi.org/10.1523/JNEUROSCI.1065-07.2007>.
- Gobes, S.M.H., Jennings, R.B., Maeda, R.K., 2019. The sensitive period for auditory-vocal learning in the zebra finch: consequences of limited-model availability and multiple-tutor paradigms on song imitation. *Behav. Processes.* <https://doi.org/10.1016/j.beproc.2017.07.007>.
- Hyland Bruno, J., Tchernichovski, O., 2019. Regularities in zebra finch song beyond the repeated motif. *Behav. Processes.* <https://doi.org/10.1016/j.beproc.2017.11.001>.
- Immelmann, K., 1969. Song development in the zebra finch and other estrildid finches. In: Hinde, R.A. (Ed.), *Bird Vocalizations*. Cambridge University Press, Cambridge, pp. 61–74.
- Johnson, J.S., Newport, E.L., 1989. Critical period effects in second language learning: the influence of maturational state on the acquisition of English as a second language. *Cogn. Psychol.* 21, 60–99. [https://doi.org/10.1016/0010-0285\(89\)90003-0](https://doi.org/10.1016/0010-0285(89)90003-0).
- Johnson, E.K., Seidl, A.H., 2009. At 11 months, prosody still outranks statistics. *Dev. Sci.* 12, 131–141. <https://doi.org/10.1111/j.1467-7687.2008.00740.x>.
- Lampen, J., Jones, K., McAuley, J.D., Chang, S.-E., Wade, J., 2014. Arrhythmic song exposure increases ZENK expression in auditory cortical areas and nucleus taeniae of the adult zebra Finch. *PLoS One* 9, e108841. <https://doi.org/10.1371/journal.pone.0108841>.
- Lampen, J., McAuley, J.D., Chang, S.E., Wade, J., 2019. Neural activity associated with rhythmicity of song in juvenile male and female zebra finches. *Behav. Processes.* <https://doi.org/10.1016/j.beproc.2017.12.003>.
- London, S.E., 2019. Developmental song learning as a model to understand neural mechanisms that limit and promote the ability to learn. *Behav. Processes* 6. <https://doi.org/10.1016/j.beproc.2017.11.008>.
- Miller, D.B., 1979. Long-term recognition of father's song by female zebra finches. *Nature* 280, 389–391. <https://doi.org/10.1038/280389a0>.
- Mol, C., Chen, A., Kager, R.W.J., ter Haar, S.M., 2016. Prosody in birdsong: a review and perspective. *Neurosci. Biobehav. Rev.* <https://doi.org/10.1016/j.neubiorev.2017.02.016>.
- Odom, K.J., Hall, M.L., Riebel, K., Omland, K.E., Langmore, N.E., 2014. Female song is widespread and ancestral in songbirds. *Nat. Commun.* 5, 3379. <https://doi.org/10.1038/ncomms4379>.
- Perez, E.C., Elie, J.E., Soulage, C.O., Soula, H.A., Mathevon, N., Vignal, C., 2012. The acoustic expression of stress in a songbird: does corticosterone drive isolation-induced modifications of zebra finch calls? *Horm. Behav.* 61, 573–581. <https://doi.org/10.1016/j.yhbeh.2012.02.004>.
- Perkes, A., White, D., Wild, J.M., Schmidt, M., 2019. Female Songbirds: the unsung drivers of courtship behavior and its neural substrates. *Behav. Processes.* <https://doi.org/10.1016/j.beproc.2017.12.004>.
- Pike, C.D., Kriengwatana, B.P., 2019. Vocal tract constancy in birds and humans. *Behav. Processes.* <https://doi.org/10.1016/j.beproc.2018.08.001>.
- Riters, L.V., Spool, J.A., Merullo, D.P., Hahn, A.H., 2019. Song practice as a rewarding form of play in songbirds. *Behav. Processes.* <https://doi.org/10.1016/j.beproc.2017.10.002>.
- Rivera-Cáceres, K.D., Templeton, C.N., 2019. A duetting perspective on avian song learning. *Behav. Processes.* <https://doi.org/10.1016/j.beproc.2017.12.007>.
- Roper, A., Zann, R., 2006. The onset of song learning and song tutor selection in fledgling zebra finches. *Ethology* 112, 458–470. <https://doi.org/10.1111/j.1439-0310.2005.01169.x>.
- Soha, J.A., 2019. Song ontogeny in Nuttall's white-crowned sparrows tutored with individual phrases. *Behav. Processes.* <https://doi.org/10.1016/j.beproc.2018.02.010>.
- Soula, H.A., Carnino, D., Fernandez, M.S.A., Perez, E.C., Villain, A.S., Vignal, C., 2019. Stress-induced flexibility and individuality in female and male zebra finch distance calls. *Behav. Processes.* <https://doi.org/10.1016/j.beproc.2018.03.018>.
- ten Cate, C., Houx, B.B., 1998. Do contingencies with tutor behaviour influence song learning in Zebra finches? *Behaviour* 135, 599–614. <https://doi.org/10.1163/156853998792897932>.
- Tobin, C., Medina-García, A., Kohn, G.M., Wright, T.F., 2019. Does audience affect the structure of warble song in budgerigars (*Melopsittacus undulatus*)? *Behav. Processes.* <https://doi.org/10.1016/j.beproc.2017.10.007>.
- Wilbrecht, L., Nottebohm, F., 2003. Vocal learning in birds and humans. *Ment. Retard. Dev. Disabil. Res. Rev.* 9, 135–148. <https://doi.org/10.1002/mrdd.10073>.
- Williams, H., 1990. Models for song learning in the zebra finch: fathers or others? *Anim. Behav.* 39, 745–757. [https://doi.org/10.1016/S0003-3472\(05\)80386-0](https://doi.org/10.1016/S0003-3472(05)80386-0).
- Yanagihara, S., Yazaki-Sugiyama, Y., 2019. Social interaction with a tutor modulates responsiveness of specific auditory neurons in juvenile zebra finches. *Behav. Processes.* <https://doi.org/10.1016/j.beproc.2018.04.003>.

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