Introductory gestures before songbird vocal displays are shaped by learning and biological predispositions

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Numerous animal displays begin with introductory gestures. For example, lizards start their head-bobbing displays with introductory push-ups, and many songbirds begin their vocal displays by repeating introductory notes (INs) before producing their learned song. Among songbirds, the acoustic structure and the number of INs produced before song vary considerably between individuals in a species. While similar variation in songs between individuals is a result of learning, whether variations in INs are also due to learning remains poorly understood. Here, using natural and experimental tutoring with male zebra finches, we show that mean IN number and IN acoustic structure are learned from a tutor. Interestingly, IN properties and how well INs were learned, were not correlated with the accuracy of song imitation and only weakly correlated with some features of songs that followed. Finally, birds artificially tutored with songs lacking INs still repeated vocalizations that resembled INs, before their songs, suggesting biological predispositions in IN production. These results demonstrate that INs, just like song elements, are shaped both by learning and biological predispositions. More generally, our results suggest mechanisms for generating variation in introductory gestures between individuals while still maintaining the species-specific structure of complex displays like birdsong.

1. Introduction

Animals produce various complex displays to communicate with their conspecifics [1]. Many of these communicative displays begin with the repetition of introductory gestures. For example, Anolis lizards produce a few introductory ‘push-ups’ or ‘tail-flicks’ before starting their head-bobbing display [2,3]; frogs and toadfish produce introductory vocalizations before their advertisement calls [4,5] and many songbirds also produce introductory vocalizations before the start of their complex songs [6–17]. The functions of these introductory gestures remain unclear, but multiple hypotheses exist based on independent observations in different animals. All of these functions relate to the main vocal display and can broadly be divided into functions that enhance the communicative aspect of the display or motor preparatory functions. For instance, under noisy conditions, the main part of the display becomes more difficult to detect and theory predicts the addition of a ‘simpler’ signal immediately before the display to ensure reliable detection [18]. This hypothesis is supported by experiments in songbirds and Anolis lizards. Territorial songbirds typically respond to playbacks of a song from a speaker. Rufous-sided towhees respond less to degraded versions of a song, but the addition of simpler introductory vocalizations before degraded song increases the magnitude of the response [19]. Similarly, Anolis lizards respond to visual head-bobbing displays of other lizards and, under low light conditions, respond more strongly to displays that begin with introductory push-ups [20].
While these studies suggest that introductory gestures add value to the communicative aspect of the display by enhancing detectability, other studies suggest that introductory gestures add value by providing recognition signals. For example, naive, young songbirds learn their songs from adults of their species and an important problem for young birds is choosing the right songs to learn. Introductory vocalizations appear to help in this selection; white-crowned sparrows can reliably learn songs of their species and even songs of other species from tape playbacks, only when these songs are preceded by the characteristic introductory whistle of white-crowned sparrows [21]. Further, this characteristic introductory whistle differs subtly between different geographical populations and birds of a particular region respond more strongly to playbacks that begin with region-specific introductory whistles, even if the songs that follow are from a different region [22]. Thus, introductory gestures could enhance the main display by increasing detectability (‘alerting’ signals) or by providing signals for recognition (‘species’/‘local-dialect’ identity).

More recent studies suggest a motor preparatory function for introductory gestures [23,24]. Motor preparation is believed to represent a brief period prior to movement, when the brain ‘prepares’ parameters of the upcoming movement [25]. The idea of motor preparation comes from the observation that movements towards a pre-specified target are faster when a delay period is introduced between target onset (representing the instruction) and the ‘GO’ cue; longer the delay, faster the onset of movement after the ‘GO’ cue suggesting ‘more’ prepared responses following longer delays [25,26]. Neural recordings in primates and rodents have shown the presence of ‘preparatory’ neural activity during this delay period, and disruption of this preparatory activity delays the movement onset [25,27]. This preparatory activity is believed to drive neural activity from a variable ‘initial’ state, at the time of target onset, to a more stereotyped, ‘final’ state from which movements can be readily generated [25]. Our recent experiments with the zebra finch, a well-studied Australian songbird [14], are consistent with a role for introductory gestures in motor preparation [23,24]. Specifically, zebra finches generally precede their songs with a series of stereotyped introductory notes (INs), which are relatively short in duration and simple in spectral content (figure 1a for an example of zebra finch INs) [8,10,14,28]. INs progress from a variable first IN to a more stereotyped last IN, just before the start of each song [23,24], similar to the progression of neural preparatory activity described in primates [25].

While the function of INs is unclear, recent studies in songbirds have also shown considerable variation in the number of

![Figure 1](https://royalsocietypublishing.org/journal/rspb/article-figs/20202796-f1a.png)

Figure 1. Mean IN number and IN acoustic structure are correlated between fathers and their normally reared sons. (a) Spectrograms of song bouts of three different zebra finches. Red shading highlights song motif and blue shading highlights INs. (b) Mean IN number varies considerably across 20 unrelated birds. Circles and whiskers represent mean and 95% confidence intervals for individual birds. Colours represent birds from (a). (c) Example spectrograms of one song bout of a father (green box) and five sons showing introductory notes (blue shaded boxes) and common motifs for each bird (red shaded boxes). Black numbers on the left indicate mean IN number for that bird. For sons, blue and red numbers represent mean similarity to father from one nest and pupils from other nests). Asterisks represents $p < 0.05$, Wilcoxon rank sum test. (d) Mean song similarity and maximum IN similarity between fathers and sons. Blue line represents chance level similarity (mean similarity between father and son). Grey circles represent individual birds, black squares and whiskers represent mean and s.e.m. for individual nests. Colours represent birds from (a). (e) Mean IN number of father versus mean IN number of son. Grey circles represent individual birds, black squares and whiskers represent mean and s.e.m. for individual nests. Red line represents regression line. Scale bars in (a) and (c) are 150 ms and 1000 Hz. (Online version in colour.)
IN repeats and IN acoustic structure between individuals of a given species [24,28–31]. (figure 1b; an example of variation seen in zebra finches). What is the source of this variation? Variation in elements of the song between individuals is a consequence of learning [8,10,32,33] and similarly, variation in IN number and IN acoustic structure could reflect variation in learning from different tutors. Another possibility is predicted by the motor preparation hypothesis. Motor preparatory activity in primates is different for different upcoming movements [25]. By analogy, if INs helped prepare the songbird brain for song production, one would expect a different number/structure of INs for different songs that follow. This would predict a correlation across birds between variation in IN number and/or structure and variation in the song that follows. Finally, variation in IN number and structure across birds could also be a result of biological predispositions similar to those involved in the production of elements of song [34,35]. Here, using natural and experimental tutoring methods, we examine these different predictions in the zebra finch. Our results demonstrate that, similar to song elements, INs are shaped by both learning and biological predispositions and suggest mechanisms for generating variation between individuals, while still maintaining the species-specific structure of complex displays, like birdsong.

2. Material and methods
All procedures at IISER Pune were conducted after approval from the Institute Animal Ethics Committee (IAEC), IISER Pune and were in accordance with guidelines of CPCSEA (Committee for the Purpose of Control and Supervision on Experiments on Animals), New Delhi. All procedures at McGill were conducted following approval from the McGill University Animal Care and Use Committee in accordance with the guidelines of the Canadian Council on Animal Care.

Zebra finches obtained from an outside vendor or bred in IISER Pune or McGill were used for all experiments. Detailed methods are present in the electronic supplementary material.

(a) Song recordings
All birds were recorded when they were adults (greater than 85 days post-hatch) and only undirected songs in the absence of any other bird were recorded. We chose to examine undirected songs because they provide a more controlled condition for quantifying IN number and structure. For example, INs before directed songs are influenced by distance from the female [36] and the quality of the stimulus [37]. In addition, the initial, softer INs can be lost in the increased background noise, typically associated with directed songs because of the movement of both birds and female vocalizations. For most birds (127/132), only files with greater than 2 s of silence before and after song bouts in a file were considered [28]. For the other five birds, we considered files with greater than 1.5 s (four birds—greater than 1.9 s; one bird—greater than 1.5 s) as we did not have enough files with greater than 2 s silence (see electronic supplementary material).

(b) Experimental groups
We used four different experimental groups in our study.

(i) Normally reared birds
A total of 16 nests were analysed with 13 nests having at least three offspring (range: 1–9). Juveniles were housed with their parents and siblings until they were 50–94 days old, after which they were transferred to the colony and housed with other males from same or different families.

For all other groups outlined below, we used naive birds (i.e. birds that had not previously learned song) to test various hypotheses about IN learning. In order to prevent song learning from their father, juvenile zebra finches were separated from their father around post-hatch day (phd) 10 (range phd 6–16) and reared with their mother and siblings until phd 35 (range: phd 34–54). Following this, juveniles were separated and housed individually in small cages (except for two birds who were housed together). These birds were then used for the different groups as outlined below.

(ii) Socially reared birds
Fourteen birds were tutored with an adult male different from their father using a social-rearing paradigm used in earlier studies [38,39] (figure 2a; n = 10 at IISER Pune and n = 4 at McGill; total n = 14 birds from 11 different nests). For the 10 birds tutored at IISER Pune, tutors were chosen after considering their mean IN number and that of the father. The absolute difference in mean IN number between father and normally reared son was 1.08 (95% CI is 0.89–1.31). To better reveal the strength of IN learning, we chose social tutors with mean IN number greater than 1.32; i.e. outside the 95% CI for the difference between father and normally reared son (mean difference in IN number between father and tutor – 2.76; range: 1.39–3.44). Birds tutored at McGill were part of a different study where song (but not IN) learning was described [39]. For these birds, INs of the tutors was not a consideration during the choice of tutor. Therefore, to investigate IN learning, only a subset of these tutored birds was analysed here. Specifically, only socially tutored birds, where recordings of both father and tutor were available and the mean difference in IN number between these two was greater than 0.5 (mean difference in IN number between father and tutor – 1.98; range: 0.52–4.63) were included in the analyses.

(iii) Playback-tutored birds
Using active tutoring methods [38,40], birds were tutored with synthesized zebra finch songs, without INs, that were played back through a speaker (figure 4a; n = 22 birds from 10 different nests) at McGill (n = 13) or at IISER Pune (n = 9).

(iv) Isolate birds
Five laboratory-bred male zebra finches (from three different nests) were reared in isolation. After birds were separated from their mother and siblings, they were kept in visual but not acoustical isolation from other birds. Earlier studies have shown that visual isolation is sufficient to prevent song learning from other birds [41].

(c) Data analysis
All analyses were conducted using custom-written scripts in Matlab (Mathworks). Scripts to generate figures used panel [42].

(i) Song segmentation and syllable categorization
Song files were segmented and labelled as described previously [23,24] (see electronic supplementary material for further details). For every bird, a motif (referred to interchangeably as song or motif in the rest of the text) was first defined as a fixed sequence of syllables that appeared consistently in a majority of song bouts. Syllables that occurred in isolation or occurred at random positions in song bouts were classified as calls. Syllable types that were repeated a variable number of times before the first motif of a song bout were considered INs. There were 68.18% (90/132) birds that had one IN type, 23.48% (31/132) had two types of INs, 5.3% (7/132) had more than two types of INs and 3% (4/
(ii) IN number calculation and associated controls
To count IN number for each bout, we started with the introductory note just before the first motif and counted backwards until either the inter-syllable interval was greater than 500 ms or the syllable was not an IN [23,24,43] (see electronic supplementary material). For birds with multiple types of INs, all types of INs were included in the calculation of IN number. For normally reared birds, we calculated correlation in mean IN number between father and son using all of the data, but used the means of the different nests to fit a regression line (figure 1c).

There was variation in the sample size of birds in each nest. To check whether this difference in sample size could influence the correlation in IN number between fathers and normally reared birds, we used a random reassignment procedure to assess the significance of the observed correlation. For this procedure, all sons were randomly reassigned to different fathers, while maintaining the actual number of birds per nest, and then the correlation between fathers and sons was calculated. This procedure was repeated 10,000 times and the 95% confidence intervals were estimated. This same randomization procedure was also used to assess the significance of the correlation between socially reared birds and their tutors. In this case, the total number of socially reared birds was maintained constant during the random reassignment procedure.

While classifying syllables as INs or motif syllables, we were not blind to the relationship between birds or the experimental group. To control for any potential biases that this might have introduced in our classification of INs and motif syllables, we also used a script-based categorization of INs and motif syllables (see electronic supplementary material). All of our comparisons of mean IN number between father and son, tutor and pupil for all groups of birds were verified using this script-based classification. All of our results using the script-based classification agreed with the results using the manual classification.

(iii) Comparison of introductory note acoustic structure
Acoustic structure similarity for both motifs and INs was computed using Sound Analysis Pro (http://soundanalysispro.com/) (see electronic supplementary material for details) [44].

(iv) Statistics
Pearson correlation coefficient was used for all correlations and was calculated using the Matlab function corrcoef. Linear fits to data were calculated using the Matlab functions polyfit and polyval. Wilcoxon rank sum test was used for calculating the significance of song and IN similarity for normally reared and playback-tutored birds and for comparing IN similarity of socially reared pupils with their fathers and social tutors. Wilcoxon sign-rank test was used for comparing song similarity of socially reared pupils with their fathers and their social tutors.

3. Results
(a) Introductory note acoustic structure and mean IN number are learned from a tutor
To examine the degree to which IN acoustic structure and mean IN number are learned, we first compared these
properties for birds that had been reared normally with their fathers \((n = 16\) nests, \(n = 65\) birds, figure 1c, electronic supplementary material, figure S1). INs (and song) of fathers were acoustically more similar to those of their sons as compared to unrelated birds (figure 1d; \(p = 0.0094\) for INs and \(p < 0.001\) for song, Wilcoxon rank sum test). Mean IN number before the song was also significantly correlated between fathers and their sons (figure 1c). This correlation in mean IN number was not influenced by the removal of individual nests from the analysis (electronic supplementary material, figure S2A) and was significantly different from the correlations obtained by randomly re-assigning individual birds to different nests (electronic supplementary material, figure S2B). Further, this correlation in mean IN number was significant even when syllables in individual birds were categorized into INs or song syllables based on pre-set rules (electronic supplementary material, figure S2C, see Methods and electronic supplementary material, figure S9). These results showed that mean IN number before the song and IN acoustic structure were correlated between fathers and their sons.

To further test the contribution of learning to IN repetition and structure, we used a social-rearing paradigm where juvenile zebra finches were kept in visual and acoustic contact with an adult male different from their father [38,39,41] (figure 2a; \(n = 14\) birds; see Methods). Importantly, mean IN number (and sometimes IN acoustic structure also) for the social tutor was different from those of the juvenile’s biological father (see example in figure 2b and Methods). INs of such socially reared birds were acoustically more similar to those of their social tutors than to those of their fathers (figure 2c; \(p = 0.028\) for INs, Wilcoxon rank sum test; \(p < 0.001\) for motif, Wilcoxon sign-rank test). Mean IN number before the song was also correlated with mean IN number of the social tutor but not of the father (figure 2d,e). The correlation with the social tutor was significantly different from that obtained by randomly re-assigning birds to different social tutors (electronic supplementary material, figure S3A, S3B) and was significant even when syllables were categorized based on pre-set rules (electronic supplementary material, figure S3C, S3D). These two sets of results indicate that the number and acoustic structure of INs are learned from a tutor (father for normally reared birds and social tutor for socially reared birds).

(b) Accurate copying of introductory notes is independent of accurate copying of song

Previous studies have suggested that INs represent motor preparation before song [23,24]. The motor preparation hypothesis predicts correlations between properties of INs and properties of songs that follow. For example, the mean number of IN repetitions could be correlated with specific features of the song. Across all birds, we compared a number of song features with the mean and variability in the number of INs (electronic supplementary material, figures S5 and S10) and could only find significant correlations between mean IN number and two song features, namely, duration of first song syllable (electronic supplementary material, figure S5B) and mean frequency of the first song syllable (electronic supplementary material, figure S5F). However these correlations were weak and much smaller than the correlations between pupil and tutor. We also compared a number of song acoustic features with the acoustic features of INs and stereotypy of IN acoustic structure (electronic supplementary material, figures S7 and S10). Among all these features, we only found weak correlations in two cases, namely, (i) mean frequency of INs and mean frequency of songs (electronic supplementary material, figures S7A) and (ii) stereotypy of IN acoustic structure and song stereotypy (electronic supplementary material, figure S10F). These results suggested that IN features were only weakly correlated, if at all, with features of the song.

The motor preparation hypothesis also predicts similar INs before similar songs representing equivalent amounts of preparation. Therefore, if a pupil copied his tutor’s songs accurately, he would also end up producing INs similar to the tutor. To rule out this possibility, we compared the accuracy of song imitation with the accuracy of IN imitation. Accuracy of song imitation was measured with Sound Analysis Pro [44] using asymmetric mode. Asymmetric mode measures acoustic similarity between the tutor song and the song of the pupil without taking syllable sequence into consideration (see Methods and electronic supplementary material, figure S8). We chose asymmetric mode to compare acoustic similarities between the song of the tutor and pupil without regard for the sequence. Symmetric mode comparisons were used for comparing INs as these are single syllables, and there is no sequence comparison involved. Across all normally reared and socially reared birds, the degree of song similarity or the degree of similarity of the first song syllable between birds and their tutors was not correlated with similarity in IN number (figure 3a, electronic supplementary material, figure S4A, S4C) or similarity in IN acoustic structure (figure 3b, electronic supplementary material, figure S4B, S4D) between birds and their tutors (father or social tutor). Overall, these results confirmed that the correlations seen in mean IN number and IN acoustic structure between tutor and tutor-reared pupil were a result of learning and not a consequence of INs functioning as motor preparation for the song.

(c) Biological predispositions in introductory note production and learning

Our results suggest that INs are learned from a tutor just like birds learn their song motifs from their tutor. Previous studies have demonstrated the presence of biological predispositions in zebra finch song learning [34,35,45]. For example, juvenile zebra finches that are individually tutored with random sequences of syllables converge on similar motif sequences [34,35]. To identify biological predispositions, if any, in IN production, we experimentally tutored juvenile zebra finches with songs that lacked INs (figure 4a, \(n = 22\), see Methods for details of tutoring). Despite being tutored without INs, juveniles tutored in this manner produced three INs, on average, before their songs (figure 4b for an example, figure 4c). The number of these INs was not correlated with those of the father (figure 4d). The acoustic similarity of these INs to those of the father was comparable to the similarity with unrelated birds (same as figure 1d), showing that these INs were acoustically different from those of the father. (figure 4d, \(p = 0.86\) for INs and \(p = 0.18\) for motif, Wilcoxon rank sum test). These results suggest more general, species-specific, predispositions in IN production rather than direct heritability from the father.

Another way to reveal biological predispositions in IN production is to analyse INs in the songs of untutored birds. As observed in a previous study [10], we found that untutored birds produce INs before their songs (\(n = 5\), see Methods for
details of untutored birds). Interestingly, the mean number of such INs produced before the song (figure 4e; $p = 0.57$, one-way ANOVA) and the duration of these INs (figure 4f; $p = 0.36$, one-way ANOVA) was similar across all categories of birds, irrespective of tutoring experience. Other features of INs differed between birds experimentally tutored without INs and birds normally or socially reared (electronic supplementary material, figure S6), highlighting the role of learning. Thus, on average, normally reared, socially reared, operantly tutored and untutored birds produced three, 60 ms long, INs before starting their songs (figure 4e,f). This bias to produce approximately three INs before the song can also be observed in the data for birds tutored with songs that contained INs. Juveniles tutored by adults that produced, on average, less than three INs tended to produce more INs than their tutor (figures 1e and 2e). On the other hand, juveniles tutored by adults that produced, on average, greater than three INs tended to produce fewer INs than their tutor (figures 1e and 2e).

4. Discussion
The complex vocal displays of many songbirds begin with the repetition of simple, introductory notes (INs) before the production of their learned song. Here, we show that INs, just like elements in the song, are learned and shaped by
biological predispositions. Specifically, using zebra finches, we show that the mean number of times an IN is repeated and the acoustic structure of INs are learned from a tutor. This learning is independent of the accuracy of song imitation and largely independent of features of the songs that follow. Finally, we reveal the existence of biological predispositions in IN production. Both untutored birds and birds tutored with songs without preceding INs, produced INs before their songs and these INs were similar in duration to the INs produced by birds tutored with songs with preceding INs. On average, these birds produced approximately three INs before starting their songs and this bias for approximately three INs was also visible in birds tutored with INs; i.e. if the tutor sang less than three INs, juveniles ended up singing a little more than their tutor while if the tutor sang greater than three INs, juveniles ended up singing a little less than their tutor. Taken together, these results demonstrate that the properties of INs are also shaped by learning and biological predispositions.

(a) Learning of introductory note number and structure
How do birds learn the number and structure of INs? Earlier studies have shown the presence of multiple strategies for learning song that involve either learning the sequence first and gradually changing the acoustic structure or learning each syllable sequentially [40,46]. Similarly, juvenile birds could potentially learn IN number first while gradually modifying IN acoustic structure. Alternatively, birds could learn the structure of INs and then gradually learn to transition to the motif after the correct number of INs are repeated. Further studies of IN development in young birds could shed more light on the process of IN learning.

(b) Relation to introductory notes of other songbirds
How do INs that precede zebra finch song relate to INs before the songs of other songbirds? As discussed earlier, many oscine songbirds produce INs before the start of their songs [6–17]. While systematic comparisons of INs across different species have not been done, it is clear that the acoustic characteristics of INs differ across species, for example INs of white-crowned sparrows are long, tonal sounds [7] unlike the short, broad-band sounds typically made by zebra finches. Our results showing the learning of IN acoustic properties and a biological predisposition for INs of a particular duration provide a simple explanation for variation across species.

(c) Functional significance of introductory notes and other such introductory gestures
What is the functional role of INs in zebra finch song? As discussed earlier, INs have been hypothesized to enhance the communicative value of song by ‘alerting’ the receiver [19,20] or by providing ‘context’ to the song [21,22]. INs have also been hypothesized to function as motor preparation [23,24]. Our data showing learning of IN number and IN acoustic structure suggests that these two aspects may not reflect motor preparation. Infact, contrary to the predictions of the motor preparation hypothesis, we found only weak correlations, if at all, between IN properties and features of the songs that follow. Our current results showing the learning of mean IN number and IN acoustic structure suggest that these two features could provide context to the song in the form of individual, regional or species identification. Learning would provide a reliable way to generate variation within specific populations and transmit this information across generations.

However, our data also reveal biological predispositions in IN production. Specifically, we observed that zebra finches are biased to produce short-duration vocalizations as INs, approximately three times before their songs, regardless of their tutoring experiences during development. All our experimentally tutored birds were isolated from their father very early in life and such short exposure to the father is not enough for song learning [47]. However, given that zebra finch embryos, in the egg, also learn some characteristics of vocalizations [48,49], our results do not completely exclude the role of a very early component of learning, in the production of repeated syllables (INs) at the start of a song bout. Interestingly, INs are also seen before the start of song in suboscine birds [13,15,17] where song is not learned and before advertisement calls in other vertebrates that produce unlearned vocalizations including frogs [4] and toadfish [5]. More generally, introductory gestures are also seen before non-vocal displays like the head-bobbing displays of lizards [2,3], and our results suggest the possible presence of conserved biological predispositions in the production of introductory gestures.

A common feature of many of these introductory gestures is repetition. Such repetition is also a feature of a number of human behaviours. For example, skilled motor behaviours, especially as part of sports, are preceded by repetitive ‘pre-performance’ routines, like ball-bouncing before a tennis serve [50]. Repetition is also a part of motor stereotypies in normal children and is often accentuated in disorders like autism [51,52]. However, these motor stereotypies are slower (lasting seconds to minutes) [51] when compared to INs or pre-performance routines that are seen in sports, suggesting less similarities with INs. What might be the function of this repetition? One possibility is motor preparation. Consistent with this idea, pre-performance routines, like ball-bouncing before a basketball free throw, appear to correlate with accurate performance; following a consistent pre-performance routine may be linked with greater accuracy with the free throw [53,54]. This suggests the possibility that INs could also have a similar function. Further experiments disrupting INs using electrical/optogenetic stimulation would help better understand whether IN repetition is necessary for song initiation.

Overall, our results demonstrate that the mean number and acoustic structure of INs that precede zebra finch song are learned from a tutor, while the production of repeated INs before the song is a biological predisposition. These results provide a novel perspective on understanding introductory gestures that are widely prevalent before animal movements. Both communicative [19–22] and motor preparatory functions [23,24] have been hypothesized for these gestures, albeit separately in different animal models and our data suggest that both functions can be served by the different attributes of introductory gestures. Irrespective of their function, a combination of learning and biological predispositions, as demonstrated by our results, suggests simple mechanisms for generating variation in introductory gestures between individuals, while maintaining the species-specific structure of complex displays, like birdsong.

Ethics. All procedures at IISER Pune were conducted after approval from the Institute Animal Ethics Committee (IAEC), IISER Pune
and were in accordance with CPCSEA (Committee for the Purpose of Control and Supervision of Experiments on Animals), New Delhi. All procedures at McGill were conducted following approval from the McGill University Animal Care and Use Committee in accordance with the guidelines of the Canadian Council on Animal Care.

Data accessibility. Matlab scripts and data for generating all of the figures are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.x95e9ph3 [55].

Authors’ contributions. S.K. and R.R. designed the experiments with inputs from J.T.S. and V.Y. and V.Y. carried out the experiments. L.S. and J.T.S. provided additional data for playback-tutored and socially tutored birds. S.K., V.Y. and R.R. analysed the data. S.K. and R.R. wrote the manuscript in consultation with V.Y., L.S. and J.T.S.

Competing interests. We declare we have no competing interests.

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