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Pattern-Induced Covert Category Learning in Songbirds

Highlights

- Words help human infants learn the boundaries for speech sound categories

- We asked whether temporal patterns shape acoustic category learning in songbirds

- Pattern learning covertly enhances categorization of species-specific song elements

- Speech acquisition may exploit top-down learning mechanisms common to many species

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In Brief

Natural patterns of speech sounds help guide lower-level phonetic category learning. Using songbirds, Comins and Gentner examine the uniqueness of top-down category learning. They find that pattern learning, but not mere exposure, enhances low-level acoustic categories. Top-down acoustic category learning is not unique to language or humans.

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Pattern-Induced Covert Category Learning in Songbirds

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SUMMARY

Language is uniquely human, but its acquisition may involve cognitive capacities shared with other species [1–5]. During development, language experience alters speech sound (phoneme) categorization [6–8]. Newborn infants distinguish the phonemes in all languages but by 10 months show adult-like greater sensitivity to native language phonemic contrasts than non-native contrasts [8, 9]. Distributional theories account for phonetic learning by positing that infants infer category boundaries from modal distributions of speech sounds along acoustic continua [10, 11]. For example, tokens of the sounds /b/ and /p/ cluster around different mean voice onset times. To disambiguate overlapping distributions, contextual theories propose that phonetic category learning is informed by higher-level patterns (e.g., words) in which phonemes normally occur [12–15]. For example, the vowel sounds /I/ and /e/ can occupy similar perceptual spaces but can be distinguished in the context of "with" and "well." Both distributional and contextual cues appear to function in speech acquisition [10–12, 16–21]. Non-human species also benefit from distributional cues for category learning [22–24], but whether category learning benefits from contextual information in non-human animals is unknown. The use of higher-level patterns to guide lower-level category learning may reflect uniquely human capacities tied to language acquisition or more general learning abilities reflecting shared neurobiological mechanisms. Using songbirds, European starlings, we show that higher-level pattern learning covertly enhances categorization of the natural communication sounds. This observation mirrors the support for contextual theories of phonemic category learning in humans and demonstrates a general form of learning not unique to humans or language.

RESULTS

The complex vocalizations (songs) of starlings follow a hierarchical acoustic structure [25–28], with short (200–800 ms long) stereotyped patterns of simple notes grouped into "motifs" (e.g., Figures 1B and S1), and longer (~1 min long) well-defined sequences of motifs organized into bouts [25]. Starling song motifs can be classified by their acoustic characteristics into four species-typical, open-ended, perceptual categories: whistles, warbles, rattles, and high frequencies [25, 26, 29–31]. The sequential patterning of motifs in bouts underlies successful individual recognition [30] and mate selection [32]. In controlled operant settings, starlings can accurately classify and generalize arbitrary motif patterns of the forms AABB and ABAB [33], where "A" and "B" represent sets of "warble" and "rattle" motifs. As in humans, the ability of starlings to generalize learned patterns is constrained by the integrity of the categorical boundaries for the pattern elements (e.g., warbles and rattles) [34, 35]. Thus, the patterning rule is defined at the level of the category, and pattern generalization requires the acoustic structure of the category to be well defined.

Here, we ask whether the acoustic structure of underlying categories, in addition to aiding pattern generalization, may also be shaped directly by pattern learning. This is the correlate to the question of whether, in humans, lexical context influences phonetic category learning. To do this, we trained one group of starlings ("pattern relevant," N = 4) using operant techniques to differentiate complex auditory patterns following the form AABB and BBAA from those that followed the form ABAB and BABA, where A and B denote natural motif categories of warbles and rattles. In addition, we trained a second group of starlings ("pattern irrelevant," N = 4) to classify the same AABB, BBAA, ABAB, and BABA motif sequences but shuffled so that the patterning rules were non-informative for correct classification (see Table 1). We then compared how rapidly pattern-relevant and pattern-irrelevant groups learned to classify the individual A and B motifs that they had already experienced. We hypothesized that the pattern-relevant experience would improve perceptual expertise for lower-level acoustic categorization. If true, then the pattern-relevant birds should show advantages in motif categorization over naive birds and over the pattern-irrelevant birds for whom the patterned motif sequences were familiar, but not behaviorally relevant.
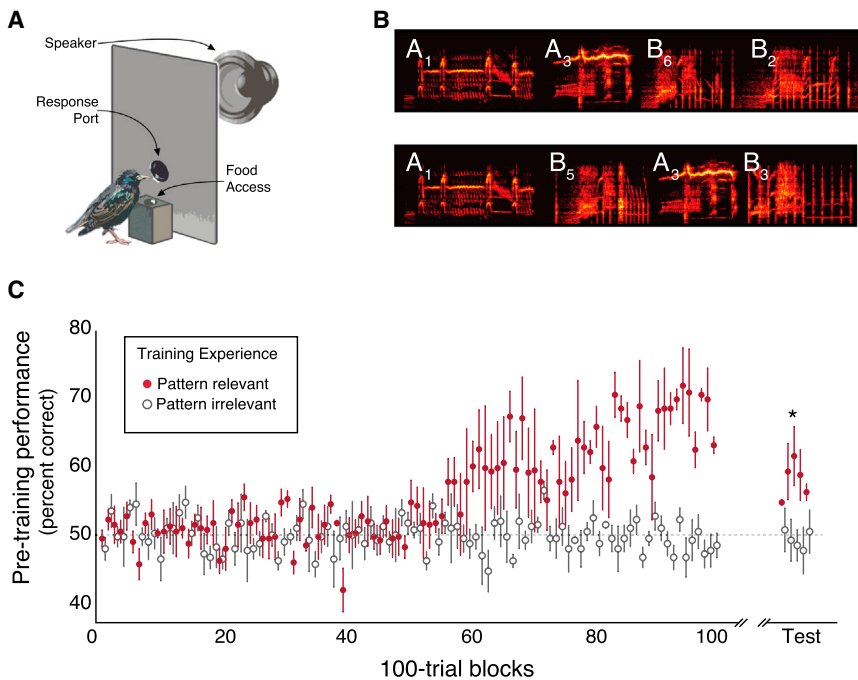
Figure 1. Pattern Training

(A) Schematic of the operant apparatus.

(B) Spectrograms typifying stimuli from the AABB and ABAB pattern classes (As denote warbles; Bs denote rattles; subscripts denote distinct motifs). In total, eight warbles and eight rattles were used to generate all types of patterned sequences in this experiment: AABB and BBAA as well as ABAB and BABA.

(C) Mean (±SEM) performance (% correct) over the course of motif pattern pre-training and subsequent generalization (labeled "test") to novel exemplars of the patterns. Dotted lines show chance performance.

and performance did not differ significantly from chance (single-sample t test; t = −0.233; p = 0.831, chance = 50%; Figure 1C).

Motif Category Learning

Following the pattern-relevant and pattern-irrelevant training, we assessed categorization of the individual warble and rattle motifs the animals had heard in the four-motif patterns. We also trained a group of experimentally naive birds on the same motif categorization task as an additional control. Birds in the pattern-relevant group showed a clear advantage in motif categorization compared to both the pattern-irrelevant and naive birds. Figure 2 shows the mean performance for the three groups across the first 600 trials, highlighting initial categorization. Over this interval, the mean performance of the pattern-relevant birds was significantly better than that for both other groups (linear mixed-effects model [LMM], $F_{(2,9)}$ = 9.96; p = 0.0052, main effect of group; Tukey's honest significant difference [HSD] post hocs: pattern relevant versus pattern irrelevant p = 0.0295, pattern relevant versus naive p = 0.0049, and pattern irrelevant versus naive p = 0.4873). Likewise, over the first 600 trials, the performance of the pattern-relevant birds improved at a significantly faster rate than that for the other two groups (LMM, $F_{(10,45)}$ = 3.551; p = 0.0016, group × training block interaction). Post hoc analyses comparing group performance in each of the first six 100-trial blocks revealed significant differences between groups emerging in blocks 5 and 6 (Bonferroni-corrected α = 0.0083; p = 0.002 and p < 0.0001, respectively; Figure 2). Birds in the pattern-relevant group reached our arbitrary learning criterion (three consecutive blocks with d′ > 1.0; Supplemental Information) in 5.5 ± 0.8 (μ ± SE) blocks, whereas birds in the pattern-irrelevant and naive groups required 14.5 ± 1.2 and 16.75 ± 4.9 blocks, respectively, to achieve the same stable, accurate motif classification.

Strong advantages for motif classification are also observed in the individual data, where two of four subjects in block 5 and four of four subjects in block 6 in the pattern-relevant group performed significantly better than expected by chance (binomial test, chance = 0.5, p < 0.05 each case). For each of the pattern-trained birds, average performance over the first 600 trials was significantly above chance (binomial test,

Pattern Training Performance

All of the pattern-relevant subjects learned to classify AABB and BBAA from ABAB and BABA patterns. The mean percentage of correct responses began improving rapidly after about 5,000–6,000 trials (Figure 1C) and by 10,000 trials was well above chance (single-sample t test; t = 11.09; p = 0.008, chance = 50%). To measure pattern generalization, we then tested subjects on 500 novel four-motif sequences, built with the same motifs and following the same patterns used during training. Mean classification accuracy during this generalization test was significantly above chance (single-sample t test; t = 3.9; p = 0.0298, chance = 50%; Figure 1C). This pattern generalization effect is observed at the individual level for three out of four subjects (bird 681: p < 0.0001; bird 716: p < 0. 002; bird 827: p < 0.0001; bird 828: p = 0.227; binomial tests where chance is 0.5). This corroborates previous results indicating that starlings recognize auditory patterns of motif categories based on their underlying temporal structures [33, 34].

For subjects in the pattern-irrelevant training group, who served as controls for sequence and motif exposure, performance never exceeded chance thresholds (single-sample t test; t = −0.696; p = 0.536721, chance = 50%; Figure 1C). To ensure that the pattern-irrelevant birds got at least as much exposure to the motifs and sequences as birds in the pattern-relevant group, we randomly paired birds between the two groups and then exposed each pattern-irrelevant bird to at least as many training trials (159.25 ± 21.47 100-trial blocks) as its paired pattern-relevant counterpart had received (119.25 ± 27.59 100-trial blocks; matched-pairs t test; t = 3.22; p = 0.0487; Figure 1C). The pattern-irrelevant subjects were also given 500 dummy pattern generalization trials, where they encountered the same generalization test stimuli as pattern-trained birds. As with their training stimuli, however, there was no fixed relationship between pattern and reward (see Table 1),

Table 1. Motif Sequence Configurations Showing the Pattern of Warbles and Rattles

Group	Stimulus Set One	Stimulus Set Two
XXYY/XYXY pattern relevant	$A_1A_8B_1B_3$, $A_2A_4B_5B_8$, $A_3A_6B_7B_6$, $A_4A_5B_8B_5$, $A_5A_1B_6B_4$, $A_6A_3B_2B_7$, $A_7A_2B_3B_2$, $A_8A_7B_4B_1$, $B_1B_3A_6A_2$, $B_2B_1A_7A_5$, $B_3B_4A_1A_4$, $B_4B_7A_3A_8$, $B_5B_2A_5A_6$, $B_6B_8A_8A_1$, $B_7B_5A_2A_3$, $B_8B_6A_4A_7$	$A_1B_5A_3B_3$, $A_2B_1A_4B_6$, $A_3B_7A_6B_8$, $A_4B_4A_5B_1$, $A_5B_6A_1B_4$, $A_6B_8A_7B_7$, $A_7B_3A_8B_2$, $A_8B_2A_2B_5$, $B_1A_6B_5A_2$, $B_2A_5B_6A_7$, $B_3A_7B_8A_3$, $B_4A_3B_3A_8$, $B_5A_2B_2A_6$, $B_6A_4B_7A_1$, $B_7A_1B_4A_4$, $B_8A_8B_1A_5$
XXYY/XYXY pattern irrelevant	$A_1A_5B_4B_8$, $A_2A_6B_3B_7$, $A_3A_7B_2B_6$, $A_4A_8B_1B_5$, $A_5B_6A_2B_3$, $A_6B_7A_3B_4$, $A_7B_8A_4B_1$, $A_8B_5A_1B_2$, $B_1B_4A_5B_2$, $B_2B_3A_6A_7$, $B_3B_2A_7A_6$, $B_4B_1A_8A_5$, $B_5A_2B_6A_3$, $B_6A_1B_5A_4$, $B_7A_4B_8A_1$, $B_8A_3B_7A_2$	$A_5A_1B_8B_4$, $A_6A_2B_7B_3$, $A_7A_3B_6B_2$, $A_8A_4B_5B_1$, $A_1B_2A_6B_7$, $A_2B_3A_7B_8$, $A_3B_4A_8B_5$, $A_4B_1A_5B_6$, $B_5B_8A_1A_4$, $B_6B_7A_2A_3$, $B_7B_6A_3A_2$, $B_8B_5A_4A_1$, $B_1A_6B_2A_6$, $B_2A_5B_1A_5$, $B_3A_8B_4A_8$, $B_4A_7B_3A_7$

Motif sequence configurations showing the pattern of warbles (As) and rattles (Bs) in each of the two stimulus sets used to train subjects in the pattern-relevant group and the pattern-irrelevant group.

Figure 2. Motif Classification

Mean (±SE) percent correct for pattern-relevant birds (red), pattern-irrelevant birds (black, filled), and naive birds (black, open) during the first six 100-trial blocks of the motif categorization task and during the final 100-trial block.

chance = 0.5, p < 0.05 all four cases). In contrast, average performance for none of the naive birds and only one of the pattern-irrelevant birds was above chance across the first six blocks (binomial test, chance = 0.5). Therefore, we conclude that auditory pattern learning, but not exposure to or rote memorization of acoustic sequences, enhances the perceptual mechanisms that underlie acoustic categorization in songbirds.

To confirm that subjects in all three groups could ultimately learn to categorize warbles and rattles with similar proficiency, we continued training all subjects past the initial 600-trial period until their performance was consistently better than chance for multiple consecutive blocks (Supplemental Information). At the end of this extended training, motif classification accuracy was similarly high in all three groups ($F_{(2,9)} = 0.28$; p = 0.7608, main effect of group in final 100-trial block; Figure 2). Thus, the motif categories are learnable for all subjects.

Our results support the idea that high-level pattern learning improves lower-level acoustic categorization. However, the poor performance of the pattern-irrelevant birds during initial training (Figure 1C) could have led to stimulus-independent response strategies that delayed subsequent acquisition for the motif classification. To examine whether pattern-relevant and pattern-irrelevant groups used the operant apparatus in similar ways, we compared several stimulus-independent response measures. During pattern training, if a subject responded incorrectly, we delivered a correction trial in which the same stimulus was repeated in the next trial and all trials thereafter until the animal responded correctly (Supplemental Information). As subjects learn the operant contingencies, the number of consecutive correction trials decreases, approaching an optimum of one. All subjects showed significant decreases in the number of consecutive correction trials over the course of pattern training (Pearson's correlation: in all eight cases, p < 0.05), and the mean rate of this decrease did not differ significantly between the pattern-relevant and pattern-irrelevant groups (unmatched t test t = −1.86; p = 0.152). By these measures, both groups
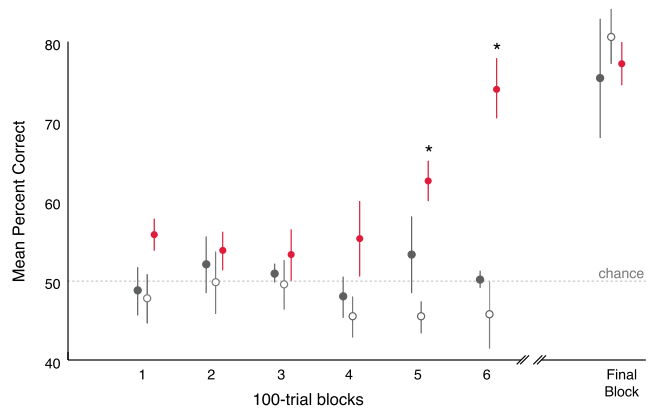
were equally adept at working the operant apparatus. Likewise, there was no significant difference between the mean reaction times for subjects in the two groups during the last five 100-trial blocks of pattern training (reaction time [RT] for Go stimuli: t = 0.642; p = 0.55; RT for NoGo stimuli: t = 1.66, p = 0.16). Thus, despite the strong difference in response accuracy (Figure 1C), both groups aligned their responses to stimulus offset. Finally, we note that during the motif classification, acquisition rates for birds in the pattern-irrelevant and naive groups did not differ significantly (paired t test, p = 0.1192, over the first 15 blocks, for which we have data from all subjects), further indicating that the pattern-irrelevant birds had not learned to ignore the song stimuli altogether, as they readily used them when their diagnostic value for the task was salient.

DISCUSSION

We show that learning to classify patterned sequences of species-specific vocalizations enhances categorization of the sequence components. This enhancement is not driven by simple exposure to or familiarity with category exemplars or sequences but rather by interaction with behaviorally relevant patterning rules operating on the acoustic categories.

Our results have important parallels to perceptual changes during the first year of human development in which infants acquire adult-like phonetic categories emphasizing the phonemic contrasts relevant to their own language environment (see [7] for review). One hypothesis for the emergence of phonetic categories is that infants learn, in an unsupervised way, the statistical properties of distributions of speech sounds along acoustic continua [10, 11, 36]. These categories could then enable access to more complex lexical information with phonemes (rather than explicit sounds) patterned into words. A second hypothesis is that phonetic category learning is shaped by the lexical (or other higher level) contexts within which speech sounds normally occur [12–15]. Distributional and contextual sources of information are not mutually exclusive, and empirical evidence consistent with both accounts has been observed [10, 11, 16, 17]. For instance, looking-time experiments with

8-month-olds suggest that infants apply word-level information to guide the perception of vowel categories [16]. Interestingly, computational studies of phonetic category learning indicate that attending to contextual cues yields more efficient phonetic category learning than distributional cues [12, 19–21], and infants are attentive to this "higher-level" information at times when phonetic categories are still developing [7, 37, 38]. Our observation of a top-down contextual learning mechanism in songbirds supports the idea that speech acquisition could co-opt general learning mechanisms not unique to humans or language.

Although we demonstrate a "top-down" effect of pattern learning on classification, it is important to note that our task does not precisely model phonetic category learning. In our study, the perceptual boundary between the warble and rattle motif categories emphasized by pattern-relevant training is well defined acoustically, and the motifs within each category are generally distinguishable. Phonemic boundaries, on the other hand, tend to parse continuous perceptual dimensions, and the elements within phoneme classes are typically indistinguishable. Likewise, the structure of reinforcement is another potentially important difference between our study and the infant studies. Given that speech-like categorical perception is well documented in non-human animals [24, 39, 40], it will be important for future studies to examine whether the top-down learning mechanisms observed here can influence more subtle, psychophysical measures of categorization acquired with unsupervised feedback.

In principle, our results could be accounted for by a mechanism that tunes perceptual representations to "category-relevant" acoustic features of the component sounds or by a mechanism that biases the associative processing of already salient features. Attention is an obvious candidate to control top-down modulation of either mechanism, as expectations gleaned from pattern structure could bias attention to specific features of sound patterns that are either about to occur or are held in working memory. This is consistent with top-down influences on phoneme perception in human adults, where ambiguous speech sounds are resolved perceptually based on the subject's knowledge of a word [41]. For example, classic psychological experiments [42] show that if a sound located in the middle of the /d/–/t/ phonetic continuum precedes "_ask," listeners will report hearing the word "task" as opposed to the non-word "dask." Contrarily, if the same stimulus precedes "_ash" subjects report hearing the word "dash" over the non-word "tash." The contributions of similar attentional and working memory processes to phonemic category learning remains an open question.

To our knowledge, we provide the first demonstration that high-level pattern learning can shape lower-level perceptual representations in a non-human animal. Starlings already serve as an important model species to investigate how experience alters the response properties of sensory neurons throughout the avian forebrain [43–50]. The strong parallels between the present results and human phonemic category learning suggest that this species may also serve as a suitable non-human model system to understand the basic biology for a range of perceptual, categorical, and learning-related mechanisms that lie at the core of infant speech acquisition [7].

EXPERIMENTAL PROCEDURES

Complete procedures are detailed in the Supplemental Information. All procedures were approved by the University of California San Diego Institutional Animal Care and Use Committee.

Twelve wild-caught European starlings (*Sturnus vulgaris*) served as subjects. Figure 1A illustrates the operant apparatus used in the Go-NoGo procedure [51] to train starlings on the four-motif pattern and single-motif classification tasks. The four-motif patterned stimuli (e.g., Figure 1B) were constructed from 16 acoustically distinct warble and rattle motifs (eight motifs per class, labeled "A" and "B," respectively; Figure S1) assembled into four-motif sequences of the form AABB, BBAA, ABAB, and BABA (Table 1). We trained one group of subjects (pattern relevant; N = 4) using 32 (out of a possible 16,384) patterned stimuli to distinguish eight AABB and eight BBAA sequences from eight ABAB and eight BABA sequences (Table 1). To control for motif and sequence exposure, we trained a second group of birds (pattern irrelevant; N = 4) to distinguish four AABB, four BBAA, four ABAB, and four BABA sequences from four AABB, four BBAA, four ABAB, and four BABA sequences (Table 1). Birds in the pattern-relevant group could solve the task by determining whether the sequence in a given trial followed the pattern XXYY or XYXY [34], where X and Y denote either A or B, but birds in the pattern-irrelevant group could not (Table 1). Stimuli for the motif categorization task were the eight warble and eight rattle motifs used to construct the patterned sequence stimuli, with a single motif presented in each trial. We compared percent correct scores across groups using an LMM and, where necessary, single and matched-pairs t tests. We analyzed individual subject data using binomial tests comparing raw numbers of correct responses in a given trial block, with chance = 50% of all responses.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and one figure and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.05.046.

AUTHOR CONTRIBUTIONS

J.A.C. and T.Q.G. designed the research. J.A.C. performed the research. J.A.C. and T.Q.G. analyzed the data. J.A.C. and T.Q.G. wrote the paper.

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