

## European starlings (*sturnus vulgaris*) discriminate rhythms by rate, not temporal patterns

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### ABSTRACT:

Humans can perceive a regular psychological pulse in music known as the beat. The evolutionary origins and neural mechanisms underlying this ability are hypothetically linked to imitative vocal learning, a rare trait found only in some species of mammals and birds. Beat perception has been demonstrated in vocal learning parrots but not in songbirds. We trained European starlings (*Sturnus vulgaris*) on two sound discriminations to investigate their perception of the beat and temporal structure in rhythmic patterns. First, we trained birds on a two-choice discrimination between rhythmic patterns of tones that contain or lack a regular beat. Despite receiving extensive feedback, the starlings were unable to distinguish the first two patterns. Next, we probed the temporal cues that starlings use for discriminating rhythms in general. We trained birds to discriminate a baseline set of isochronous and triplet tone sequences. On occasional probe trials, we presented transformations of the baseline patterns. The starlings' responses to the probes suggest they relied on absolute temporal features to sort the sounds into "fast" and "slow" and otherwise ignored patterns that were present. Our results support that starlings attend to local features in rhythms and are less sensitive to the global temporal organization. © 2021 Acoustical Society of America.

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### I. INTRODUCTION

Auditory timing is an important cognitive function for animal communication. Some animals, like humans and songbirds, produce elaborate, organized acoustic signals that contain rich temporal information (e.g., music, birdsong). In order to make sense of and potentially respond to incoming signals, the brain perceives and encodes the temporal organization of sound in real time. The brain can reduce the computational load associated with temporal processing of quasi-periodic signals by anticipating the timing of future events (Haegens and Zion Golumbic, 2018). For instance, when humans listen to rhythmic sounds such as music, they may detect the presence of a predictable, regular pulse known as the beat (Drake *et al.*, 2000; Large and Palmer, 2002). Once a beat is induced in the listener, the brain uses the beat to anticipate the timing of future events and to guide the timing of synchronous motor behaviour (Rankin *et al.*, 2009). Beat perception is a universal musical skill in humans that is essential for dance and performance (Large, 2000). Although beat perception ability has been studied extensively in humans, our understanding of its underlying neural mechanisms is incomplete and its evolutionary history remains poorly understood (Leow and Grahn, 2014; Patel, 2014). Cross-species studies of animals closely related to humans (e.g., non-human primates) may indicate when

and how beat perception ability first emerged in humans or their ancestors which could provide clues as to the origins of musicality (McDermott and Hauser, 2005; Fitch, 2006). Examining the beat perception abilities of more phylogenetically distant species (e.g., birds) could facilitate broader comparative analyses of temporal processing abilities (Kotz *et al.*, 2018).

One problem with testing whether non-human animals are capable of perceiving the beat is the lack of available testing methods, given that animals can not be explicitly instructed to perform behavioural tasks in the same way humans can. Several experiments have indexed beat perception by measuring motor entrainment—the capacity of animals to achieve and maintain temporal synchrony of body movement with the beat of rhythmic stimuli (i.e., “dancing” to the beat). For entrainment-based animal studies to provide convincing evidence of beat sensitivity, they require the subject to demonstrate an ability to flexibly adjust the timing of body movement (e.g., head bobbing, foot lifting) to maintain synchronization with the beat position over a range of tempi and across discrete stimuli, such as metronomes or music (see Patel *et al.*, 2009b for a detailed description of entrainment methodology). Patel (2006) discovered the first incidental evidence of beat perception in a non-human animal by demonstrating motor entrainment in a cockatoo parrot. Patel proposed the vocal learning and rhythmic synchronization hypothesis (herein “vocal learning hypothesis”) to explain why apparently only a few species,

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including humans and parrots, seem to be able to both sense the beat and synchronize their body movement to the beat. Like beat perception ability, imitative vocal learning is a rare trait among animals. The brains of vocal learning animals, such as humans, parrots, and songbirds, have specialized auditory-motor circuits that support tight temporal coupling of auditory input with motor control of vocal production (Jarvis, 2007). The vocal learning hypothesis suggests that auditory-motor connectivity in vocal learning animals is integral to the neural mechanism responsible for beat perception and synchronization. The hypothesis predicts that vocal non-learning species are not able to perceive the beat, which has indeed been supported by results of numerous tests of vocal non-learning animals including non-human primates, pigeons, and penguins (Zarco *et al.*, 2009; Haggmann and Cook, 2010; Fobe, 2017). However, this prediction was contradicted when positive evidence for beat perception was found in a vocal non-learning sea lion (Cook *et al.*, 2013). On the other hand, experiments testing for beat perception ability in vocal learning animals have been limited to only humans, parrots, and zebra finches. A handful of studies have indexed beat sensitivity by measuring motor entrainment (e.g., Hasegawa *et al.*, 2011; Patel *et al.*, 2009a; Schachner *et al.*, 2009). Relatively fewer studies have examined beat perception ability directly (without measuring entrainment), but they have begun to shed light on prerequisites for beat perception, such as sensitivity to rhythmic patterns. Of particular relevance are experiments by ten Cate *et al.* (2016) that tested regularity perception in captive budgerigars and zebra finches. ten Cate *et al.* (2016) trained birds using a Go/No-go procedure to discriminate between a regular and irregular pattern consisting of two different tones. Next, they tested birds on various tempo transformations of the two patterns. Accuracy on the discrimination was reduced for both species following the tempo transformations, suggesting that birds attended to local temporal features and not the global regularity. However, some individuals did show additional sensitivity to patterns, which provides some evidence that budgerigars and zebra finches have the capacity to attend to both local and global features in rhythms.

In the present study, we set out to investigate whether European starlings (*Sturnus vulgaris*), a songbird species capable of open-ended song learning and heterospecific vocal imitation, can perceive the beat in auditory rhythms, and test how starlings perceive temporal features of sound sequences. Starlings produce elaborate, rhythmic songs with hierarchical structure (Pavlova *et al.*, 2005). Starlings, like humans, learn new vocalizations throughout their lifespan (Mountjoy and Lemon, 1995). Many aspects of auditory cognition have been studied in starlings, and as a result, much is known about how starlings perceive frequencies, intensities, harmonies, and fine spectral structure (see Hulse *et al.*, 1992 for a review). Studies of starlings' ability to perform auditory pattern discriminations have shed light on the species' sensitivity to multiple levels of temporal organization in sound. Starlings are adept at learning absolute

durations of single intervals (Maier and Klump, 1990). Braaten and Hulse (1993) demonstrated that starlings can use grouping principles when perceiving stimuli that contain multiple discrete events. The capacity of starlings to learn hierarchical grammar rules has been shown with experiments that used artificial arrangements of the species' vocalizations (Gentner *et al.*, 2006). Starlings can discriminate regular from irregular patterns of auditory elements and can segregate auditory streams based on temporal cues (Hulse *et al.*, 1997; Itatani and Klump, 2011). Starlings' ability to segregate overlapping auditory stimuli into streams has been shown using combinations of heterospecific and conspecific vocalizations as well as sequences of pure tones that differed in frequency (Hulse *et al.*, 1997; MacDougall-Shackleton *et al.*, 1998). Starlings are capable of recognizing conspecific individuals based on vocalizations, a task that may depend on memorization of associations, pattern recognition, and perhaps specific vocal characteristics (Gentner and Hulse, 1998). Overall, past research on auditory perception in starlings suggests that starlings are capable of focusing their auditory attention on a variety of properties of complex sounds including temporal structure. Like most non-human animals, starlings typically attend to individual elements of auditory sequences rather than global patterns, but some authors have suggested that the capacity to learn pattern rules does exist in this species and may be recruited under specific circumstances (Gentner and Hulse, 2000).

A few studies have probed starlings' sensitivity to tempi in rhythms. Hulse *et al.* (1984b) showed that starlings are capable of discriminating rhythmic vs arrhythmic auditory patterns and could transfer the discrimination to patterns with interval durations modified in a ratio or additive manner. Their results suggest that the starlings classified patterns on the basis of being rhythmic or not, maintained this strategy across changes in stimulus rate, and attended to relative relationships among the durations that composed the patterns. Hulse and Kline (1993) trained two groups of starlings on discrimination between pulse trains with different tempi (with half of the subjects discriminating between 4 and 8 pulses/s and the other half between 8 and 16 pulses/s). In one experiment, they presented probes with various tempi other than the baseline tempi. Their results showed that birds in both groups responded on a relational basis to changes in tempi. In a second experiment, they tested the same birds on either a relational transfer (i.e., from "4 left and 8 right" to "8 left and 16 right") or a non-relational transfer (i.e., "4 left and 8 right" to "16 left and 8 right"). They found that the birds that underwent a relational transfer performed better than did the non-relational transfer group. The authors concluded that the starlings classified the sounds on a "faster than" or "slower than" basis. Haggmann (2013) conducted a series of comparative experiments with starlings and humans (vocal learning) and pigeons (vocal non-learning) to examine how each discriminated between fast and slow tempi in auditory and visual rhythmic patterns. The humans and starlings processed auditory patterns similarly with little difficulty discriminating between fast and

slow, which showed sensitivity to the onset of audible beats, processes that were stimulus-dependent when a variety of sounds were used, and dominance of audition over vision in cross-modal transfers. Taken together, these studies provide evidence that starlings are sensitive to tempi as well as certain relative cues in rhythms. However, further study is needed to establish whether starlings are capable of perceiving an auditory beat, particularly when the beat is derived from temporal accents rather than being directly audible.

In two experiments, we attempted to investigate first whether European starlings can perceive the beat in auditory rhythms, and second, how starlings process rhythm timing in general. We trained wild-caught birds on a series of two-choice auditory discriminations. Our first experiment examined whether birds could be trained to discriminate between metrical patterns that contained or lacked a regular configuration of temporal accents (i.e., a beat) to test a prediction of the vocal learning hypothesis that starlings, being a vocal learning species, are capable of beat perception. In a second experiment, we returned the same birds to a separate pattern discrimination that they learned previously. We then presented various transformations of the learned patterns to probe the strategies and specific cues that starlings used to discriminate temporal auditory patterns.

## II. GENERAL METHOD

### A. Subjects

We used eight experimentally-naive, adult European starlings (*Sturnus vulgaris*, four male, four female) captured near Port Rowan, Ontario (42°41'54.8"N, 80°24'35.7"W). The sex of each starling was determined based on the dimorphism of bill colouration at the time of capture. Our care and treatment of the birds adhered to the guidelines of the University of Western Ontario and the Canadian Council on Animal Care (CCAC) and all procedures were approved by the institution's Animal Care Committee (protocol 2016–105). We individually housed birds within wire cages inside a single room at 20 °C and a light timer mimicked the natural photoperiod. Each cage contained a variety of perches and environmental enrichment. The birds' diet consisted of Purina chick starter supplemented with hardboiled eggs and mealworms, initially fed *ad libitum* in the home cage. Throughout the experiments, we controlled the birds' daily food to maintain them at 85% of their maximum recorded body weight. During testing, birds received a rationed amount of food in their home cage following the completion of an experiment session; food was not available prior to the sessions.

### B. Apparatus and procedure

Birds worked inside one of four modular test boxes (30 × 24 × 29 cm; Med Associates Inc., St. Albans, VT) inside a sound attenuating chamber (audiometric testing booth) located in a separate room away from their home cage (Fig. 1). The boxes contained a trial initiation key, a panel containing two response keys, a house light, a

computer speaker used to present auditory stimuli (Logitech s11; Fremont, CA), and a food hopper filled with a mixture of the birds' base starter diet and mealworms. The trial initiation key was situated in the center of the wall opposite of the response panel. The response panel included two circular keys (diameter 2.5 cm) located to the left and right of a port (5 × 6 cm) through which the bird accessed the food hopper. A microcontroller connected to a computer running MED-PC IV software (Med Associates Inc.) controlled input from the keys and output to the hopper, house light, and speaker. When the computer registered a correct key peck, a light inside the port turned on and the food hopper shifted upwards to an open position, enabling the bird to access its contents for the length of a fixed feeding interval. When the computer registered an incorrect key peck, the small house light that dimly illuminated the box would shut off, leaving the bird in darkness for a fixed time-out period (25 s).

### C. Shaping and training

We trained birds to use the operant apparatus over several sessions. Birds habituated to the boxes with the food hopper fixed in the open position. Then the birds learned to access the contents of the food hopper within an allotted feeding interval (first 30 s, then 15 s, then 7 s, and finally 3 s) as the hopper alternated between the open/closed position. Next, we trained birds to peck the three keys in the chamber. We baited a single key at a time by taping a mealworm onto the reverse side of the key's transparent plastic backing. When birds pecked the baited key, the food hopper shifted into the open position. Once birds were reliably pecking the baited key, we removed the mealworm cue in the following session.

First, birds learned to peck the trial initiation key. Second, when birds pecked the trial initiation key, the speaker played a 7 s sound stimulus (described below). Food delivery occurred only if the birds pecked the baited left

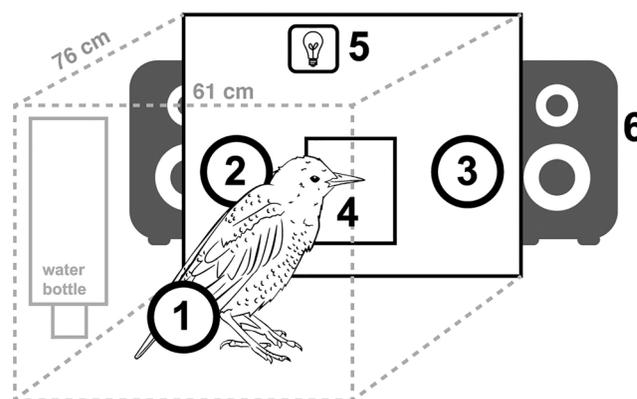


FIG. 1. Schematic showing the organization of the testing apparatus. Subjects peck the trial initiation key (1) to trigger a sound stimulus presentation from the speakers (6) positioned approximately 8 cm behind the box. Subjects then peck the left (2) or right (3) response key. Correct responses cause the food hopper (4) to shift into the open position for a feeding interval. Incorrect responses cause the house light (5) to turn off for a timeout period.

response key within 8 s after the stimulus ended. Third, when birds pecked the trial initiation key, an alternate sound stimulus played, but now the right response key was baited. Birds performed several alternating sessions in which only the left or right key was reinforced. In the final stage of peck training, when birds pecked the trial initiation key one of the two sound stimuli was presented at random. Pecks registered by the correct associated key for each sound were rewarded, and incorrect pecks produced no effect.

We attempted to train starlings to delay pecking keys until after the sound stimulus ended using a variant of the shaping procedure reported by Braaten and Hulse (1993). However, the starlings showed a tendency to peck at the response keys repeatedly throughout stimulus presentations and were unable to learn to delay their responses after multiple training sessions. Therefore, we modified the procedure such that only the first response following the end of the stimulus would be registered by the program and produce feedback. The program did not record additional key pecks produced by the birds prior to the registered response.

Next, we gradually introduced a timeout period following incorrect responses which increased in duration (5, 10, 25 s) across three sessions. If the birds pecked the incorrect key after the stimulus ended, the house light in the chamber turned off for 25 s. Each timeout was followed by a single correction trial which repeated the stimulus from the previous error trial. If the birds failed to peck either response key within 8 s after the stimulus ended, the trial was recorded as an omission of a response; no feedback was provided, and a correction trial followed. Correction trials would repeat until the bird produced the correct response. Data from correction trials were not included in the analyses.

Each bird was tested once daily starting at the same time in sessions lasting exactly two hours. At the end of the sessions, birds were returned to their home cages. We weighed the contents of the hoppers and deducted the amount of food consumed by each tested bird from its daily allocated food. The remainder of daily food was provided to the starlings approximately two hours after returning to their home cages to ensure the birds remained motivated towards the end of the sessions.

### III. EXPERIMENT 1—DISCRIMINATING STRONG AND WEAK BEAT PATTERNS

We trained starlings on a two-choice sound discrimination to test their ability to perceive the beat. We designed rhythm stimuli based on the Povel and Essens (1985) model of temporal accent perception, keeping with previous experimental research on beat perception in humans (e.g., Grahn and Brett, 2007; Bouwer *et al.*, 2018). We used a computer program based on the model to generate patterns fitting criteria for inclusion in one of two rhythm categories that formed the basis of the discrimination. To explain how these stimuli were created, a brief summary of the model is provided below.

#### A. Rhythms with a stronger or weaker beat

Humans' ability to detect the beat in musical rhythms is related to their perception of accents—instances when a single note is emphasized relative to others in its immediate context. Some accents in music coincide with physical variations in sound (e.g., the amplitude or frequency of notes). However, according to the Povel and Essens (1985) model, the accents that humans perceive in music that give rise to the beat are purely psychological and are derived by the listener from the temporal organization of rhythm. The position of *temporal accents* within a rhythm follow rules based on the relative arrangement of events: accents are perceived on events that are relatively isolated in time, on the second event in groupings of two, and on the last event within a perceptual grouping of three or more events.

The model predicts the inter-beat interval—referred to as a clock unit—that best fits the overall temporal structure of the rhythm by maximizing the number of beats (regular ticks of the clock) that align in time with the position of accented events. The temporal unit of the best-fitting clock and the strength of the resulting beat can be predicted by amalgamating contributions of each accented and unaccented event in the rhythm. This amalgamation of positive and negative evidence for and against the fit of a particular clock (from accented and unaccented events respectively) is represented by a counterevidence score. In other words, counterevidence against a clock indicates how poorly the regular ticks of that clock would align with the temporal position of accented events in a given rhythm. A high counterevidence score suggests that the listener will not perceive a beat in the unit of that clock.

The two metrical categories of rhythms for our first discrimination experiment differed from each other only in terms of counterevidence against a 4-unit clock. The first metrical category, *metric simple*, included rhythms in which temporal accents occurred consistently on every fourth event onset. Therefore, counterevidence scores against the fit of a 4-unit clock to metric simple rhythms were always minimal (0 or 1). The metric simple rhythms produce a stronger sense of a regular beat in humans which coincides with duple meter, the most common form of metrical structure in Western music (Vuust and Witek, 2014; van der Weij *et al.*, 2017). The second metrical category, *metric complex*, included rhythms that may contain some accented events, but unlike metric simple, the temporal positioning of accents in metric complex was not systematically regular. Metric complex rhythms produce counterevidence scores that are higher (we included only patterns with a score against a 4-unit clock of 5 or greater) because of unaccented events that align with clock ticks and clock ticks that do not coincide with events at all. Humans generally experience difficulty perceiving a beat in metric complex rhythms, so the beat that may be found in these patterns can be described as weaker.

The patterns that comprise rhythms used in this experiment, each a unique combination of inter-tone intervals, are

represented with integer notation (Fig. 2). Each integer denotes the relative duration of a single inter-onset interval within a sequence of 6, 7, or 8 identical 1500 Hz 80 ms sinusoidal tones with 10 ms on/off ramps. We selected this frequency because it is close to the mean peak power in a starling song and is within the normal perceptual range for starlings. The patterns were generated based on the Povel and Essens (1985) model using a procedure described elsewhere (Samuels, 2018). In summary, the patterns each belonged to one of two metrical categories based on whether or not they produce a strong sense of the beat in human listeners. The basic unit of inter-onset intervals within the patterns was 1 = 0.22 s (2 = 0.44 s, 3 = 0.66 s, 4 = 0.88 s, 5 = 1.10, 6 = 1.32). The base unit duration was selected to correspond roughly to the upper range of durations of inter-note intervals found in recordings of starling song. We closely matched the composition of the patterns across the categories so that subjects could only discriminate metric simple from metric complex if they detected the presence of regular temporal accents.

### B. Experiment 1 methods

The experiment was originally intended to include three stages: training, transfer, and testing. In the initial training stage, birds were introduced to the discrimination between metric simple and metric complex, starting with one rhythm from each category. We began training three pilot birds on a discrimination between one metric simple (42231) and one metric complex (23142) rhythm (Fig. 2) paired with the left and right response keys, respectively. We chose these two sequences comprised of the same intervals to mitigate the risk of starlings learning to discriminate stimuli based on their overall rate or duration or using a unique local feature like a single interval. However, across 25 sessions of discrimination training (following initial habituation and

shaping) the pilot birds did not show signs of improvement in response accuracy (see Sec. III C).

To diagnose whether this apparent failure resulted from an issue with the metrical stimuli, or due to the training procedure itself, we transferred the three birds to a second, easier discrimination between an isochronous pattern of tones (66666) and a pattern of tone triplets (226226) that were not derived from the Povel and Essens model. This discrimination has been learned successfully by starlings in other experiments (MacDougall-Shackleton *et al.*, 1998) and therefore served as a positive control here. We began training five additional experimentally naive starlings on the isochronous/triplet discrimination. The eight birds performed isochronous/triplet trials across multiple sessions until they reached the criterion to advance, at which point they transferred back to the simple/complex discrimination to resume training.

### C. Experiment 1 results and discussion

The three pilot birds did not improve accuracy on the initial simple and complex discrimination over 25 sessions of training. However, when the pilot birds and five additional experimentally-naive birds next transferred to the isochronous-triplet patterns, all eight successfully learned the discrimination and exceeded chance level responding (mean 25.8 sessions, standard deviation, SD ± 10.6) (Fig. 3).

Seven of the eight birds failed to learn the discrimination between a single metric simple and metric complex pattern despite each completing over 10 000 trials from across 36 to 51 sessions (Fig. 4). This result is consistent with the earlier failure of the three pilot birds to learn a discrimination of the same patterns. While two of the starlings showed modest improvement after many thousands of trials, only Bird 4 exceeded chance-level responding after 20 training

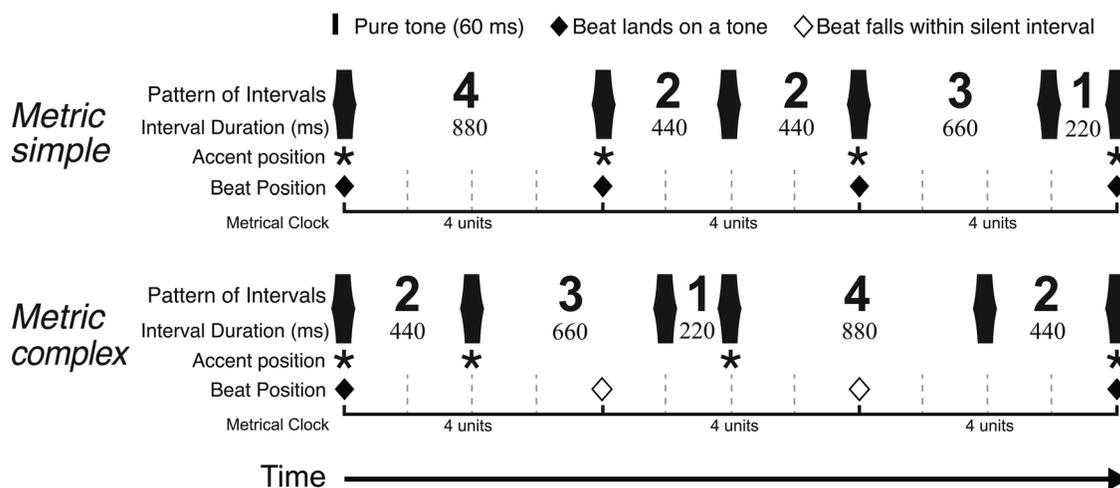


FIG. 2. Temporal configuration of the first metric simple (42231) and metric complex (23142) patterns presented as training stimuli for the first beat-based discrimination. Black bars represent the position of identical pure tones. Integers between bars represent relative durations of inter-onset intervals, with absolute interval durations shown below in seconds. In metric simple (strong beat) patterns, temporal accents are perceived at regular intervals that coincide with a 4-unit metrical clock. In metric complex (weak beat) patterns, the position of temporal accents is irregular, and accents do not align with a 4-unit clock, resulting in some beats that fall on silent intervals between tones.

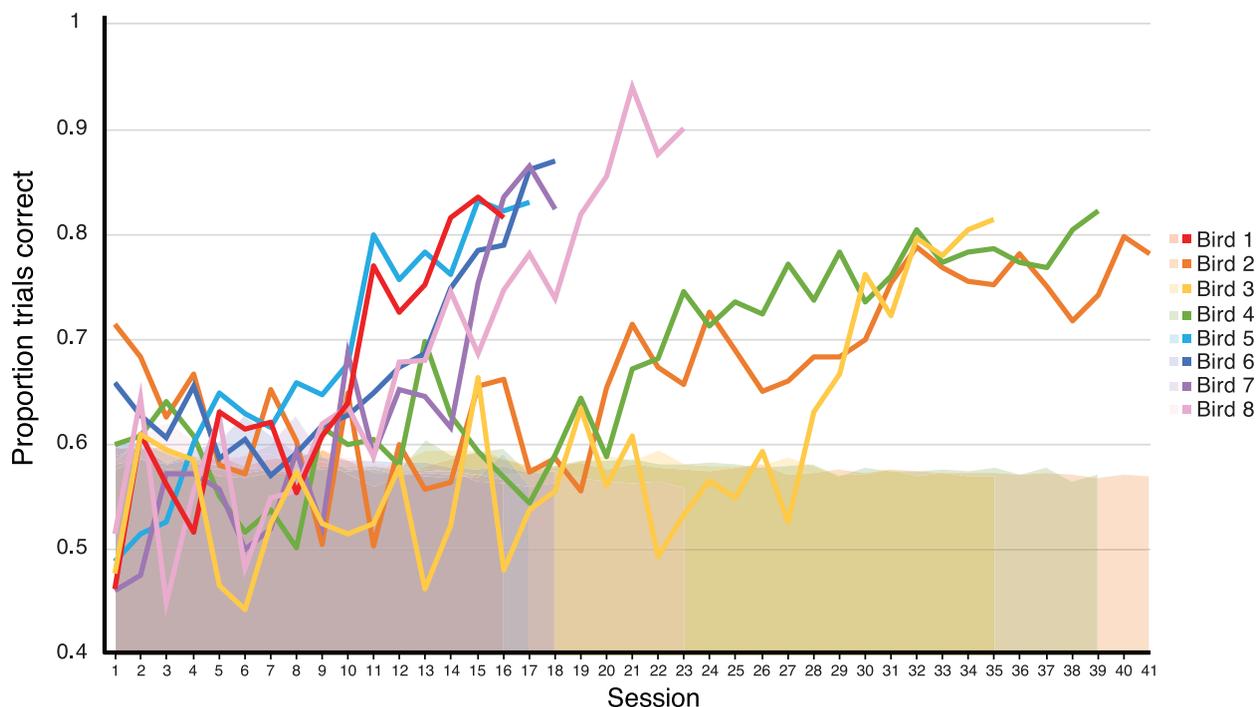


FIG. 3. (Color online) Proportion of choice responses correct for eight European starlings on the first isochronous (666666) and triplet (226226) discrimination. Each coloured line represents an individual bird. Chance level calculated per session for each bird is depicted in the shaded area. All eight birds met the criterion to advance.

sessions. Bird 4 continued to improve in accuracy until it met the criterion to advance after 46 sessions.

Bird 4 next proceeded to a discrimination of two novel stimuli that we presented on random trials ( $P = 0.25$ , respectively) intermixed with the previous metric simple and metric complex. These novel patterns (14232) and (22413) were also derived from the same parent set of intervals as the previous two and were paired with the left and right response keys respectively. When the two new patterns were introduced, Bird 4's accuracy dropped markedly. Discrimination of the two previously learned patterns failed, and Bird 4 failed to learn associations for the two new stimuli across 17 sessions (Fig. 5).

In summary, the starlings were able to learn the isochronous-triplet discrimination, consistent with results reported by MacDougall-Shackleton *et al.* (1998). However, the same birds were unable to discriminate between the pair of metric simple and metric complex pattern despite feedback over many thousands of trials.

#### IV. EXPERIMENT 2: DISCRIMINATING TEMPORAL PATTERNS

In experiment 1, we were unable to proceed past the training phase of the beat perception experiment because the starlings failed to learn the first discrimination. To a human listener, the metric simple rhythm 42231 and metric complex 23142 sound obviously different, so why were starlings unable to discriminate between these two patterns even after many thousands of trials? Solving this discrimination, even by rote memorization, would appear to be straightforward

given that the same birds were able to discriminate isochronous from triplet temporal patterns using the same equipment and general procedures. In experiment 2, we explored the specific cues that starlings use to discriminate temporal patterns. We examined whether starlings use relative timing, such as relationships between tone and silent durations that form patterns, or if starlings instead rely solely on absolute timing, such as the absolute length of individual pattern elements.

A relative sense of time is critical for humans' perceptions of temporal structure in sounds. By sensing relationships between durations that make up a rhythm, humans can detect patterns that are perceptually invariant across changes in rate. For instance, humans can easily recognize a familiar tune if played back faster or slower than normal; even when absolute temporal information is mitigated, the relative structure of the pattern remains the same. Relative timing is also a prerequisite skill for beat perception. If a piece of music is sped up or slowed down, humans can maintain their sense of the beat and can compensate for changes in rate to maintain motor synchronization to the beat. There is limited experimental evidence to suggest that songbirds can process temporal sequences on a relative basis (van der Aa *et al.*, 2015; Hulse *et al.*, 1984b).

##### A. Experiment 2 methods

The experiment procedure used here remained mostly unchanged from experiment 1. We returned the eight starlings to the discrimination between the isochronous (66666) and triplet (226226) patterns they successfully learned

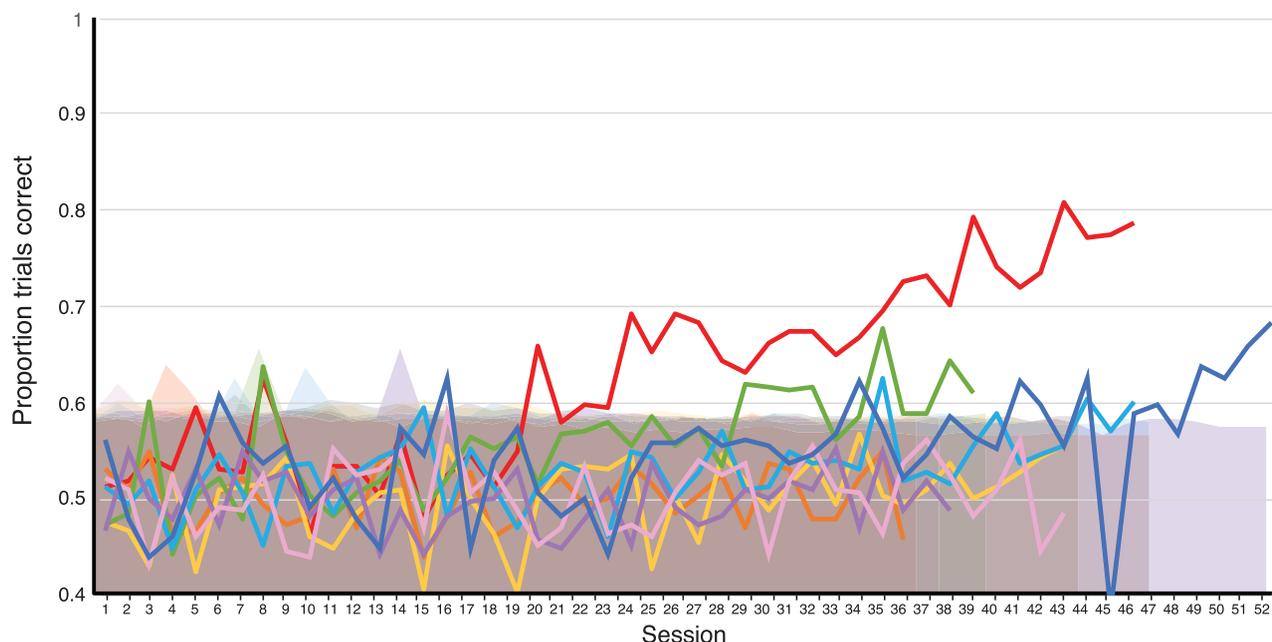


FIG. 4. (Color online) Proportion of choice responses correct for eight European starlings on the first metric simple (42231) and metric complex (23142) discrimination. Each coloured line represents an individual bird. Chance level was calculated for each session for each bird using a binomial test and is depicted in shaded area. Bird 4 shown in red was the only starling that reached the criterion to advance after 46 sessions.

before as a new baseline discrimination. We calculated birds' accuracy on the baseline isochronous-triplet discrimination as a proportion by dividing the number of correct responses from the total number of trials in each session, excluding correction trials. Once the birds were responding above chance level, we gradually introduced a variable ratio reinforcement schedule such that on occasional random trials ( $P = 0.20$ ) responses produced no feedback and instead lead directly into the next trial. We next replaced these unreinforced trials with probe trials in which we presented novel probe stimuli, with a single probe stimulus used in a testing session. The order of probe stimulus presentations was

pseudorandomized for each bird. If no response was registered on a probe trial, the next trial began without correction. Each testing session (session with probe trials) was separated by two sessions in which no probes were presented so as to maintain the birds on the baseline discrimination with the feedback schedule in place.

We created 12 unique probe stimuli by applying various transformations to the intervals that comprised the isochronous and triplet baseline patterns while matching the overall length of the stimuli (11–13 s) using the same base interval ( $1 = 0.22$  s) as in experiment 1. (Table I; Fig. 6). These stimuli were designed so that the starlings' responses could

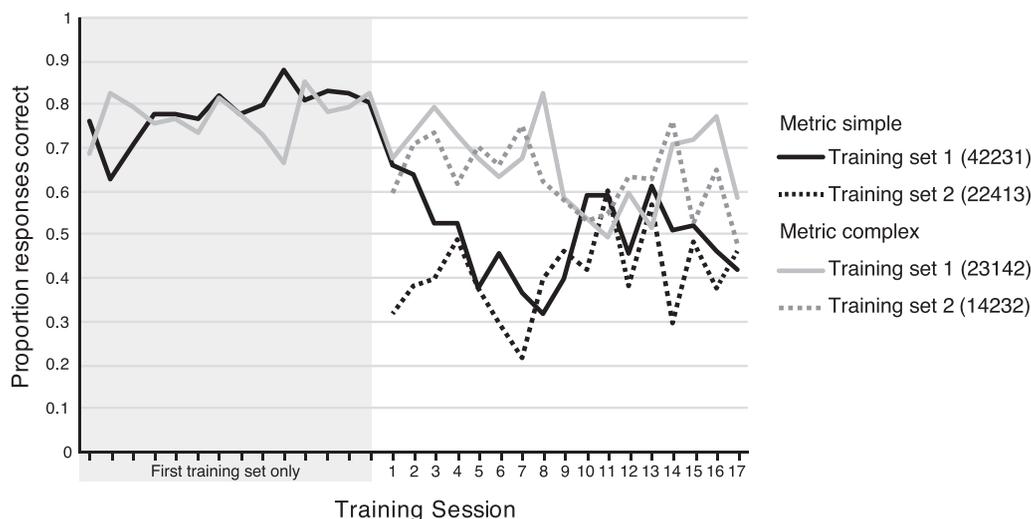


FIG. 5. Choice responses to two sets of metric simple and metric complex training stimuli by Bird 4. Initial responses following introduction of the second training set suggest the second metric complex (solid gray) was treated as similar to the first (dashed gray), while correct responses to the first and second metric simple (black) declined.

TABLE I. Baseline patterns and probe stimuli presented to starlings in the second experiment.

Pattern name (transformation relative to baseline)	Sequence of intervals	Mean interval duration (relative)	Mean interval duration (s)
Baseline isochronous	6 6 6 6 6 6	6	1.32
Baseline triplet	2 2 6 2 2 6	3.33	0.73
Isochronous (fast)	2 2 2 2 2 2	2	0.44
Isochronous (fast)	3 3 3 3 3 3	3	0.66
Isochronous (fast)	4 4 4 4 4 4	4	0.88
Isochronous (slow)	9 9 9 9 9 9	9	1.98
Triplet (fast)	1 1 3 1 1 3	1.67	0.37
Triplet (fast)	2 2 3 2 2 3	2.33	0.51
Triplet (slow)	2 2 9 2 2 9	4.33	0.95
Triplet (slow)	5 5 8 5 5 8	6	1.32
Triplet (slow)	4 4 12 4 4 12	6.67	1.47
Dyads	2 6 2 6 2 6	4	0.88
Alternating dyads	2 6 6 2 6 6	4.67	1.03
Quadruplets	2 2 2 6 2 2 2 6	3	0.66

reveal specific features of the stimuli that the birds were attending to. Several of the probes consisted of tempo transformations in which all of the intervals contained within the isochronous and triplet patterns were uniformly lengthened or shortened to produce faster and slower versions while maintaining the relative temporal structure. If the starlings used relative temporal cues, we predicted they would recognize faster/slower transformations as containing familiar patterns. Or, if instead the starlings relied on absolute temporal cues, they would relate the probes to a baseline pattern by matching individual temporal features such as the duration of single intervals or the overall rate of the stimuli. For example, consider the probe 222222: the interval “2” occurs only in the baseline triplet pattern 226226 but not in the baseline isochronous pattern 666666. If the starlings use a strategy based on absolute timing, they would match 222222 with the baseline triplet, whereas if their strategy was based on relative temporal relationships, they would recognize a pattern in 222222 and match it with the baseline isochronous.

We also considered the possibility that the starlings might use perceptual groups in their strategy. Braaten and Hulse (1993) examined whether starlings can segregate auditory streams and found some evidence for the birds perceptually grouping discrete events. Two of our probe stimuli contained ratios of intervals that might be conducive to the starlings forming groupings besides triplets. If the starlings’ strategy was based on grouping principles, we expected them to associate the probes containing tone quadruplets (22262226) and dyads (262626) with the baseline triplet pattern. In three other probes, we altered the 1:3 ratios of intervals in the baseline triplet pattern to test whether the birds recognized the presence of triplets even when the relative temporal distance within or between triplet groupings was modified. For example, the pattern 558558 more closely resembled the isochronous baseline pattern (666666) in terms of absolute durations but contained relative relationships more consistent with a triplet configuration (226226).

For each probe trial, we categorised the response as “isochronous” if the bird responded to the same key for which it was rewarded for responding to isochronous stimuli in baseline trials, or as “triplet” if the bird responded to the same key for which it was rewarded for responding to triplet stimuli in baseline trials. Responses from each bird to each of the probe stimuli were collated in Microsoft Excel and encoded as the proportion of probe trials in a test session that the bird responded “isochronous.” Response data were analyzed using IBM SPSS Statistics for Mac, Version 20.0.

**B. Experiment 2 results and discussion**

All eight birds met the accuracy criterion for a second time on the isochronous-triplet discrimination, requiring fewer sessions on average than in the first experiment (mean = 16.9 sessions; SD = 8.6 sessions). Between 50–60 probe trials occurred in each testing session. In general, birds produced consistent responses to most of the probes, relating each to one of the two baseline patterns throughout a test session. However, one subject (Bird 2) was unable to maintain accuracy on the baseline discrimination upon

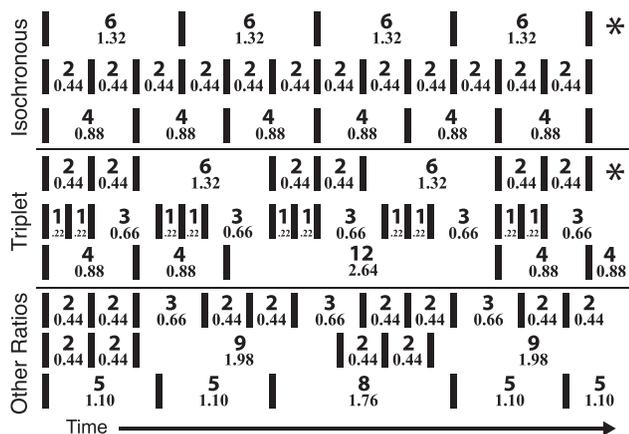


FIG. 6. Temporal configuration of a subset of stimuli presented during experiment 2. Black bars represent the position of identical pure tones. Integers between bars represent relative durations of inter-onset intervals, with absolute interval durations shown below in seconds. Asterisks indicate the two baseline patterns, shown with faster and slower transformations.

repeat presentations of the probe stimuli. Data from this bird was therefore excluded from analyses.

A repeated-measures analysis of variance (ANOVA) found no significant difference in responding to the probes across subjects, so proportions of isochronous responses to each of the probes were averaged across the seven birds. That there was strong agreement among the seven birds suggests that they shared a similar strategy.

A simple linear regression was used to assess whether the proportion of isochronous responses was based on stimulus rate, calculated as the mean duration of intervals within each probe. The proportion of responses to the isochronous key was significantly predicted by stimulus rate [ $R^2 = 0.742$ ;  $F(1,10) = 28.79$ ,  $p < 0.001$ ; Fig. 7]. As the rate of the probe stimuli decreased (i.e., the mean interval length of the patterns increased) the birds treated the probes as similar to the isochronous baseline, regardless of the pattern the probes contained.

Overall, the starlings' responses suggest they discriminated the probes based on overall rate; birds related slower probes to the baseline isochronous pattern (66666) and faster probes to the baseline triplet pattern (226226).

## V. GENERAL DISCUSSION

Several studies have found evidence that songbirds can discriminate auditory patterns with similar qualities to the rhythms used in these experiments. For example, [ten Cate et al. \(2016\)](#) trained zebra finches and budgerigars to discriminate between regular and irregular pulse strings and found that the birds mostly failed to generalize the

discrimination across changes in tempo, which the authors attributed to birds focusing on local temporal features (e.g., duration, inter-onset interval) rather than global patterns (e.g., inter-beat interval). [Hulse et al. \(1984b\)](#) conducted a series of operant experiments with starlings and demonstrated that the species can discriminate between regular and random pulse strings; unlike the budgerigar and zebra finch study, starlings were able to generalize the discrimination when certain stimulus properties were modified. This was taken as evidence for starlings being sensitive to the relative durations that made up the patterns ([Hulse et al., 1984a](#); [Humpal and Cynx, 1984](#)). In a later experiment by [MacDougall-Shackleton et al. \(1998\)](#), starlings were trained to discriminate between an isochronous pattern from a triplet ("gallop") pattern. Our finding that starlings can discriminate isochronous/triplet agrees with the results of that study.

To our knowledge, no previous research has explored whether songbirds can perceive temporal accents or the beat in auditory rhythms. We designed the metric simple/complex discrimination to test whether non-human animals are capable of beat perception. If an animal is able to learn the discrimination, as we have shown humans are capable of doing without explicit instructions ([Samuels, 2018](#)), this positive result would provide evidence that the tested species can sense the regular arrangement of accents that in humans gives rise to the perception of a beat. This test paradigm could provide the necessary means to examine beat perception ability in a variety of non-human animals using a method that can be standardized, is reproducible, and is

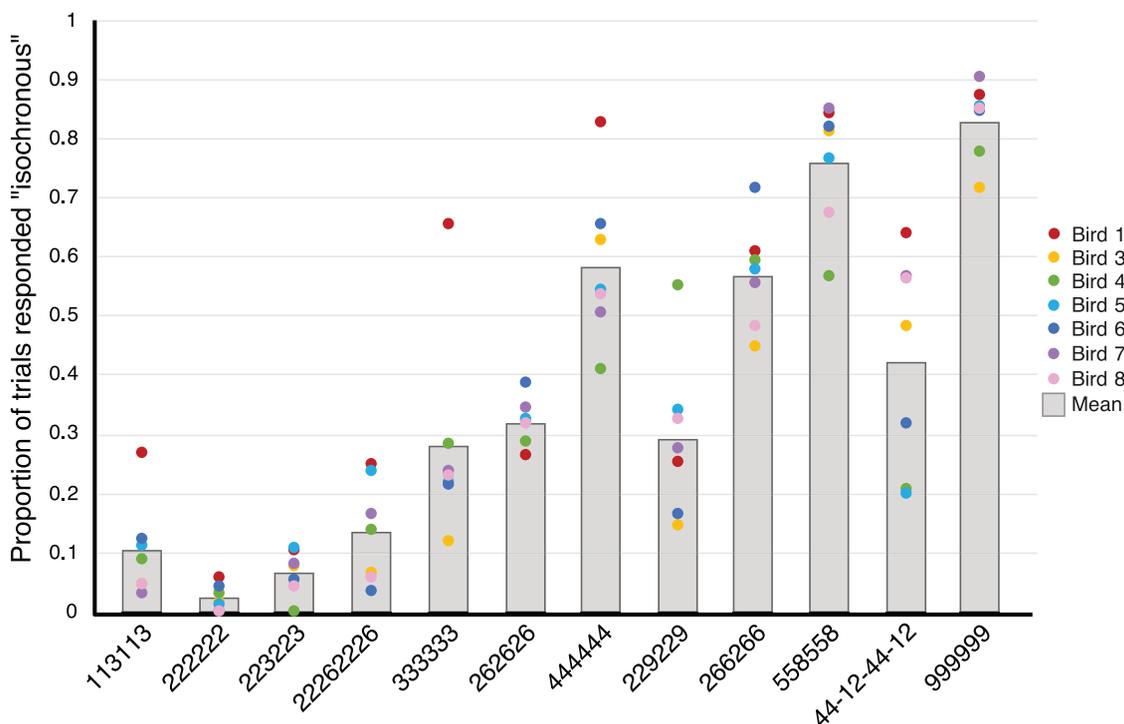


FIG. 7. (Color online) Responses of seven European starlings to 12 probe stimuli in the second experiment. Bird 2 failed to maintain the baseline discrimination when probe stimuli were introduced, so data collected from that bird were discarded. Black bars show averaged responses across subjects expressed as the proportion of trials in a session that birds responded "isochronous." Probe patterns are ordered by increasing mean interval length.

comparable across species. Moreover, this method could test beat perception ability directly without relying on the capacity of animals to perform motor entrainment behaviour, which despite being a common method used in comparative studies, is fundamentally separate from perception ability. In the present case, a positive result would lend support to the vocal learning hypothesis which predicts that songbirds, as vocal learning animals, have the required auditory-motor circuitry for beat perception.

We were unable to carry out the beat perception experiment with starlings because the birds did not progress past the training stage and were unable to learn the initial discrimination of just two metrical patterns. This premature failure surprised us at the time because we expected that the two patterns could be discriminated by the birds using any of multiple low-level features. For example, the metric simple 42231 and metric complex 23142 each start and end with different intervals. Considering the large number of trials that the birds performed, each time receiving feedback following a response, we expected that they might adopt a simple memorization strategy. Although the birds fared worse overall than we anticipated, we observed wide variability across individuals in learning of the first training discrimination, similar to differences reported by [ten Cate \*et al.\* \(2016\)](#). We speculated that this variability could be attributed to birds using different strategies to perform the task. For instance, the seven birds that failed to learn the simple-complex discrimination may have attended to an irrelevant feature of the stimuli that was indistinguishable between the pair. Selective attention to the regular structure of temporal accents that occurs in metric simple, but not metric complex stimuli would have been critical for the starlings to ultimately learning the task, but a lack of sustained attention on the patterns could have contributed to the failure to complete training. As noted above, the birds showed a tendency to repeatedly peck at the keys during stimulus presentations. It is possible that during this pecking the birds ceased attending to the simple and complex stimuli for long enough to recognize differences in the patterns they contained.

Bird 4 was the only starling that learned to discriminate the first two metric simple and complex patterns. When Bird 4 advanced to a discrimination of four patterns, its responses to the previously learned patterns were differentially affected: it treated the novel metric complex 14232 as similar to the previous metric complex 23142, and both were categorized with greater (above chance level) accuracy than the two metric simple patterns 42231 and 22413 ([Fig 4](#)). However, after several sessions, the discrimination failed and Bird 4 no longer responded accurately to any of the patterns. Given that only four patterns were presented, it seems likely that whatever strategy Bird 4 developed was feature-based rather than conceptual or was based purely on memorization. We speculate that Bird 4 may have attended to some local feature contained in both of the two metric complex patterns but not in the metric simple, such as a grouping of consecutive intervals 1 and 4. Still, this limited data obtained from a single subject says little about the strategies

that starlings use for discriminating temporal patterns in general, so this became the focus of our follow-up experiment.

Our second experiment aimed to characterize how starlings use temporal cues for rhythm discriminations, which may shed light on why the metric/simple complex discrimination failed. If the starlings discriminated probe stimuli based on relative timing, we expected they would pick up on the overall structure of patterns contained in the stimuli. An isochronous probe stimulus made up of uniformly longer or shorter durations than the learned baseline isochronous would still be recognized as containing the same pattern since the relative ratios between the intervals remain constant. Similarly, a triplet probe stimulus would be recognized as a triplet even if the intervals it contained were uniformly longer or shorter than the learned baseline.

The starlings' responses to the probe stimuli indicate that this was not the case in our experiment. Birds related 99999 but not 22222 or 33333 to the baseline isochronous pattern 66666, and related 113113 but not 44-12-44-12, to the baseline triplet pattern, 226226. So, if not on the basis of relative temporal structure, how did the subjects perceive and categorize the patterns? Overall, the strategy which best explains the observed trends is one based on absolute temporal information. When a probe stimulus was fast (as in 222222 or 113113), the birds treated it as a triplet, the faster of the two baseline patterns; when a probe stimulus was slow (as in 999999 or 44-12-44-12) the birds related it to the slower baseline isochronous pattern (666666). When a probe stimulus was structurally dissimilar to either of the baseline patterns (with relative temporal cues mitigated, as in 223223 or 262626) the birds still associated slower stimuli with the isochronous baseline and faster stimuli with the triplet baseline. In summary, the starlings most likely discriminated the temporal patterns in our experiment using some mental approximation of stimulus rate, such that when they heard a probe they recognized as relatively slow, they pecked the left (isochronous) key, and when a stimulus was relatively fast, they pecked the right (triplet) key. This trend is consistent with results of experiments with starlings reported by [Hagmann \(2013\)](#) in which birds categorized auditory rhythms on a faster/slower basis. However, even when the rate of the full stimulus is identical (e.g., 444444 vs 262626; or 333333 vs 22262226) there is some variation in responses of individual birds. It seems plausible that certain birds could have also attended to additional factors such as the presence of regularity, but we do not have evidence here to say so definitively.

Although we cannot determine when in the course of these experiments the starlings began processing the rhythms they heard on an absolute temporal basis, we speculate that an early adoption of this strategy could explain why the birds failed to learn the metric simple/complex discrimination. If the starlings were biased to only look for absolute temporal differences between metric simple and metric complex, they would have found none because the metric simple 42231 and metric complex 23142 share identical

intervals, and by extension, the same overall rate and duration. We selected these two patterns as the initial exemplars of the metric simple and metric complex categories precisely for this reason: to discourage the birds from listening for absolute temporal features. Even if the birds first attempted to find differences in absolute temporal cues in the metric simple and complex, repeated negative feedback across thousands of trials should have discouraged them from continuing to apply that strategy. That the starlings seemingly did not resort to using pattern-based or relative temporal cues might suggest they lack the capacity to sense relationships between durations, at least in the minimalist tonal rhythms used here. However, the birds' failure to learn a training discrimination between metric simple and complex should be interpreted with caution considering the small number of test stimuli and lack of equivalence across the two experiment procedures cannot allow us to draw firm conclusions about how metrical patterns might be perceived by starlings in general.

Designing auditory stimuli to be less artificial and more consistent with species-specific sensitivities might improve the outcome of future tests of beat perception ability using the metric simple/complex discrimination. For instance, the rate of our stimuli and the duration of inter-tone intervals that comprised the patterns may not have been suitable for auditory pattern perception by starlings. We selected the rate of the metric simple and complex patterns to fall within the range of tempi that humans perceive a beat to facilitate future comparative studies. However, these stimuli were relatively slow and simplistic compared to the fast-paced, variable vocalizations of starlings. The longest inter-tone silent interval contained in the metric simple and complex patterns was 0.88 s, and some of the probe stimuli in the second experiment contained intervals with even longer durations. It may be that the starlings perceptually segregated events on either end of these longer intervals, which could have interfered with their ability to detect global patterns. If beat perception occurs in non-human animals, there may be differences in the range of possible rates at which other species can sense the beat. We constructed rhythms for our experiments using identical sinusoidal tones because they are used widely in human and animal psychophysical experiments and because the plainness of tones was unlikely to result in distractions or unintended learning outcomes. Perhaps stimuli for testing beat perception could be made more naturalistic and suitable for testing starlings if they are constituted with more appropriate sound elements, such as clicks or rattles, which occur in the species' vocal repertoire. Other investigations of pattern learning in this species have used faster rates and some have incorporating recorded elements of starling vocalizations (e.g., Braaten and Hulse, 1993; Comins and Gentner, 2010; Comins and Gentner, 2014).

Humans will expect events in rhythms to fit with duple meter, which is statistically the most common metrical structure in music (Vuust and Witek, 2014; van der Weij et al., 2017; Temperley, 2010). Listeners predict future accented events will align in time with a duple beat (Grahn

and Rowe, 2013). Many previous experiments tested beat perception ability in humans with rhythms containing regular accents in alignment with a metrical 4-unit clock (e.g., Grube and Griffiths, 2009; Shmulevich and Povel, 2000; Shu-Jen et al., 2013). For the purposes of our exploratory work with starlings, we assumed that the birds would be sensitive to this form of metrical structure. However, other possible configurations of metrical structure exist that were not considered here. For instance, triple meter, in which the basic unit consists of three beats, is also common in Western music (Randel and Apel, 1986). It remains unknown if non-human animals show preferences for metrical structure outside of forms preferred by humans.

Before testing for beat perception ability across species, additional research is needed to understand how birds perceive metrical structure and accents in general. The applicability of clock-induction models to temporal processing in non-human animals has not yet been established, and it is unknown whether birds perceive temporal accents at all. We elected to explore beat perception ability in starlings in the first experiment because temporal processes and auditory pattern learning in this species have already been thoroughly described by past research. However, it is possible that starlings and other passerine species differ in how they parse the temporal organization of patterns in sound, in which case our finding that starlings prefer to use absolute temporal cues may not be representative of all passerines. It seems likely that specialization of mechanisms for auditory temporal processing could exist among passerines given the tremendous interspecific variation in vocal behaviour in this avian group. Future research could pursue species comparisons among passerine species and between passerines and other avian groups, such as vocal learning parrots or hummingbirds and vocal non-learning pigeons, by using standardized testing procedures to gain further insight into the generality of capabilities and strategies for solving temporal pattern discriminations, especially as they compare to equivalent processes in humans (e.g., Haggmann, 2013). For instance, a recent study compared responses of zebra finches and budgerigars to auditory patterns containing accents that were produced with slight variations in the intensity of certain tones that were also presented at a different frequency from the standard tone (ten Cate et al., 2016). Those experiments found no evidence for perceptual grouping or pulse perception attributable to accents. The current paper can be differentiated from work by ten Cate et al. (2016) by its exclusive use of identical tones and its focus on discriminating patterns based on temporal accents, rather than intensity accents, in the metric simple-complex experiment. Starlings' sensitivity to intensity or frequency accents as they relate to beat position has not yet been explored, and so a comparison with zebra finches and budgerigars is not possible at this time, but this could provide a promising avenue for future research to probe beat sensitivity in this species.

One way that research on accent perception by non-human animals could be carried out is by adapting methods used previously to study accent perception in humans, such

as tasking the subject with adjusting the volume of a tone to match the perceived intensity of target accented event in a rhythm (Povel and Okkerman, 1981). Another procedure could train animals to discriminate offbeat tones in metric simple patterns, and then test generalization of the discrimination to metric complex patterns to assess differences in performance across the two metrical categories. If subjects can discriminate offbeat tones in metric simple patterns but not in metric complex, this would provide evidence for sensitivity to an underlying beat pattern. Characterizing how non-human animals perceive different types of accents and metrical structure will help future studies to design species-appropriate stimuli for testing hypotheses about temporal processes such as beat perception.

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