



Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

The perception of regularity in an isochronous stimulus in zebra finches (*Taeniopygia guttata*) and humans

Jeroen van der Aa^a, Henkjan Honing^b, Carel ten Cate^{a,c,*}^a Behavioural Biology, Institute of Biology Leiden, Leiden University, P.O. Box 9505, 2300 RA Leiden, Netherlands^b Amsterdam Brain and Cognition, Institute for Logic, Language and Computation, University of Amsterdam, Netherlands^c Leiden Institute for Brain and Cognition, Leiden University, Netherlands

ARTICLE INFO

Article history:

Received 14 October 2014

Received in revised form 24 February 2015

Accepted 24 February 2015

Available online xxx

Keywords:

Zebra finches

Auditory discrimination

Rhythm

Tempo

Music

ABSTRACT

Perceiving temporal regularity in an auditory stimulus is considered one of the basic features of musicality. Here we examine whether zebra finches can detect regularity in an isochronous stimulus. Using a go/no go paradigm we show that zebra finches are able to distinguish between an isochronous and an irregular stimulus. However, when the tempo of the isochronous stimulus is changed, it is no longer treated as similar to the training stimulus. Training with three isochronous and three irregular stimuli did not result in improvement of the generalization. In contrast, humans, exposed to the same stimuli, readily generalized across tempo changes. Our results suggest that zebra finches distinguish the different stimuli by learning specific local temporal features of each individual stimulus rather than attending to the global structure of the stimuli, i.e., to the temporal regularity.

© 2015 Published by Elsevier B.V.

1. Rhythm perception in humans and non-human animals

Detecting regularity in an auditory stimulus such as music, and consequently synchronize to it (e.g., by dancing or foot tapping) is considered a fundamental musical skill: It allows humans to dance and make music together (Wallin et al., 2000). This skill has been referred to as beat perception and synchronization (Patel, 2006), beat induction (Honing, 2012), or pulse perception and entrainment (Fitch, 2013). Furthermore, it is considered a spontaneously developing (Winkler et al., 2009), music-specific (Patel, 2008), and species-specific skill (Fitch, 2009).

One way to gain more insights on the evolution of this common and widespread human skill is through comparative research on musicality, a term that is used to indicate the cognitive and biological mechanisms that underlie the perception and production of music, as opposed to musical activities that are shaped by culture (Honing and Ploeger, 2012; Honing et al., 2015). Beat induction can be defined as the cognitive mechanism that supports the perception of regularity in a varying rhythmic stimulus (Honing, 2012) and is thought to be a fundamental aspect of musicality, among

metrical encoding of rhythm, relative pitch and tonal encoding of pitch (Peretz and Coltheart, 2003; Trehub, 2003).

One suggested requirement for beat induction is the ability of vocal production learning, referred to as the vocal learning and rhythmic entrainment hypothesis (Patel, 2006). Both vocal learning and rhythmic entrainment depend on the tight coupling between the auditory and the motor systems to perceive and produce the regularity. And indeed, recent studies have revealed that, when given a complex rhythmic stimulus, those species that were able to extract the beat and entrain their movements to it were vocal learners (Hasegawa et al., 2011; Patel et al., 2009; Schachner et al., 2009) although a recent example seems an exception to this rule (Cook et al., 2013). Nevertheless, since no evidence of rhythmic entrainment was found in many other vocal learning species (including dolphins, seals, and songbirds; Hoeschele et al., 2015; Patel et al., 2009; Schachner et al., 2009), vocal learning may be necessary, but not sufficient for rhythmic entrainment and the perception of regularity (cf. Merchant and Honing, 2014).

Most evidence for beat induction comes from observing rhythmic synchronization of movements to a musical stimulus (Cook et al., 2013; Hasegawa et al., 2011; Patel et al., 2009; Schachner et al., 2009). Although regularity detection is a requirement for such rhythmic entrainment, absence of the entrainment does not automatically entail absence of regularity detection. It might well be that the animals notice the regularity in the auditory input, but lack the ability to entrain their own motor behavior with it.

* Corresponding author at: Leiden University, Behavioural Biology, Institute of Biology Leiden, Sylviusweg 72, P.O.Box 9505, 2300 RA Leiden, Netherlands. Tel.: +31 71 5275040.

E-mail address: c.j.ten.cate@biology.leidenuniv.nl (C.t. Cate).

Hence, a profitable strategy to obtain insight in the ability for beat detection in animals may be to focus on their ability to perceive the rhythmicity in auditory stimuli. In this study we use a go/no go paradigm to explore regularity detection in the absence of rhythmical entrainment. Using such a paradigm, it was found that pigeons (*Columba livia*) have great difficulty with detecting the regularity in artificially constructed rhythmical stimuli (Hagmann and Cook, 2010), although in a closely related dove genus, the collared dove (*Streptopelia decaocto*), rhythm seems to be a very salient and important cue for inducing responses to species specific coo-vocalizations (Slabbekoorn and ten Cate, 1999). Another study using the go/no go paradigm found indications of rhythm perception in the European starling (*Sturnus vulgaris*; Hulse et al., 1984). In that experiment starlings were trained to make a distinction between an isochronous rhythmic pattern and a set of irregular rhythms. When the birds were subsequently asked to respond to stimuli that were tempo-transformed training stimuli (i.e., scaled to a different inter-tone duration), the birds readily generalized to the novel tempos. This indicates that, similar to humans, starlings were able to utilize the relative time interval information present in the stimuli to perform the task. In other words: the birds discriminated the stimuli not by attending to the specific features (like duration of intervals) of the stimuli, but by a higher order feature, the regularity of the pattern. As far as we are aware, no experiment since then tested the ability to respond to tempo changes in any songbird species.

In the current study we focus on regularity detection as a fundamental component of the cognitive process of beat induction. We did this by comparing regularity detection in zebra finches (*Taeniopygia guttata*) and humans. Zebra finches are vocal learning songbirds. They are a model species worldwide for studies on vocal learning and its neurobiological basis (e.g., Haesler et al., 2004; Jarvis, 2007) as well as for studies on auditory perception and discrimination (e.g. van Heijningen et al., 2009; Verzijden et al., 2007; Weisman et al., 1998), making them a relevant model for studies on regularity detection. Also, a recent study (Lampen et al., 2014) showed differences in ZENK expression in several brain nuclei (NCM, CMM, Tn) between zebra finches exposed to repeated song motifs in which the elements were regularly spaced and motifs with an irregular spacing of elements. Furthermore, a study by Nagel et al. (2010) showed that zebra finches trained to discriminate two songs maintained the discrimination when the songs were compressed or expanded up to about 25%. These studies suggest that zebra finches might also be able to generalize tempo changes in artificial isochronous stimuli. The addition of human participants served to establish whether our stimuli were able to induce the perception of regularity in humans.

2. Experiment 1: Single training stimuli

While earlier studies using a go/no go procedure have demonstrated that zebra finches are able to discriminate artificial stimuli differing in number, sequence, intensity or frequency profile of vocal elements (e.g., Lohr and Dooling, 1998; Spierings and ten Cate, 2014; Verzijden et al., 2007; Weisman et al., 1998), it so far has not been examined whether they can discriminate stimuli in which the relative timing of otherwise identical elements has been varied. Therefore, in our first experiment, we trained the birds to distinguish between one isochronous and one irregular stimulus. Upon demonstrating that the birds are able to make the discrimination, they were tested with novel stimuli that were rhythmically identical to the training stimuli though differing in tempo. If the discrimination is based upon having learned the regular-irregular distinction, then we expect the birds to treat the test stimuli similar to the training stimuli of the same category. Alternatively, the

birds might have learned the precise features of the training stimuli and treat other stimuli proportional to their similarity with the training stimuli, i.e., they might show some generalization in their responses, but no evidence of a categorical discrimination between regular and irregular stimuli.

2.1. Methods

Methods, as described below, are similar to earlier go/no go studies on zebra finches (e.g. van Heijningen et al., 2009, 2013).

2.1.1. Animals

Four adult zebra finches (at least 120 days old, 2 females, and 2 males) from our breeding colony at Leiden were trained and tested in individual operant conditioning chambers using a go/no go procedure. The birds were naïve to the setup and training. In the breeding colony, adult birds were housed in same-sex aviaries on a 13.5:10.5 L:D schedule at 20–22 °C. Cuttlebone, drinking water, and commercial tropical seed mix (Tijssen, Hazerswoude) enriched with minerals were available ad libitum. The birds received a limited amount of egg food and sprouted seeds twice a week.

2.1.2. Apparatus

During the training and tests, the birds were individually housed in operant conditioning cages (70 (l) × 30 (d) × 45 (h) cm) made of wire mesh with a plywood back wall. Temperature and L:D schedule were identical to the breeding colony. Cuttlebone and water were available ad libitum, commercial tropical seed mix was used for positive reinforcement. Each cage was in a separate sound attenuated room, so the birds could not hear or see each other. The floor was covered with sand and grit. A fluorescent tube on top of the cage emitted daylight spectrum light (Lumilux DeLux Daylight, Osram) on a light/dark schedule identical to the breeding colony except when the birds responded to a no go stimulus (see go/no go procedure) resulting in the light being switched off temporarily. The back wall contained a food hatch and two red pecking keys, each containing a red LED (see go/no go procedure). The pecking keys and food hatch could be reached from wooden perches, with four additional perches to enable hopping behavior. A small mirror was placed on a side wall as cage enrichment. Sound stimuli were played via a loudspeaker (Vifa MG10SD109-08) located 1 m above the operant conditioning cage and calibrated to an output of 70 dB (SPL meter, RION NL 15, RION) at the food hatch. A custom made control unit (Leiden University) was connected to the fluorescent tube, loudspeaker, pecking keys, and food hatch, to control the go/no go procedure and register the birds' key pecking behavior during this procedure. Food intake was monitored daily, and before and after the experiment the birds were weighed to monitor their health.

2.1.3. Go/no go procedure

The zebra finches were trained in a go/no go operant procedure with food as a reward. In the operant cage, the left sensor was illuminated with a red LED. A peck on this sensor resulted in a sound stimulus and also activated the right sensor, indicated by switching on the LED of this sensor. In 50% of all cases, the sound was a 'go' stimulus (S^+) after which the bird had to peck the right sensor (go-response) within 6 s. Subsequently, the food hatch opened for 10 s, and the bird was able to eat. In the other 50% of the cases (in randomized order) that the bird pecked the left sensor, a 'no go' sound (S^-) was played. If the bird subsequently pecked the right sensor within 6 s, the cage light was switched off for 15 s.

To learn the go/no go procedure, birds were pre-trained with a natural song from a database as S^+ and a 2 kHz tone as S^- (equalized on RMS 1.0 and ramped with 3 ms) of equal duration (0.58 s), which were constructed in PRAAT (version 4.5.08, www.praat.org). Upon

reaching criterion performance (>75% go-response after hearing S^+ and <25% go-response after hearing S^- , on at least two consecutive days), the pre-training stimuli were replaced by the training stimuli for the experiment (transfer on the third day).

After the birds had reached the performance criterion on the pre-training, the pre-training stimuli were replaced by the training stimuli (S^+ isochronous and S^- irregular). The overall ratio of positive and negative sounds played was 1:1. At the end of this training phase (when the criterion for reaching discrimination had been reached again), probe sounds were used to assess whether the birds generalized the discrimination to novel isochronous and irregular stimuli. These probe sounds, which were presented in 20% of the trials, were not reinforced. The birds were exposed to the training stimuli during the remaining 80% of the trials. In order to get the bird used to the occasional lack of reinforcement after responding, we first removed reinforcement for 20% of the training stimuli for a few days. This lack of reinforcement of the training stimuli was maintained until the bird reached the learning criterion for two consecutive days. Hereafter the probes were introduced. A test was completed once the birds finished 40 trials of each probe type. The probes are presented using conditional probability, all probes were presented once before presented a second time.

2.1.4. Stimuli

We constructed our rhythmic stimuli using a single, repeated tone in the range 1.5–5 kHz and with an average inter-onset interval (IOI) for the training sounds of 175 ms. These characteristics were chosen to match the perceptual sensitivity of zebra finches. They are most sensitive to frequencies within the range of 1–5 kHz (Okanoya and Dooling, 1987), while an IOI of 175 ms is in the same range as the tempo in which they produce their songs, which contain around 7–9 element/s.

The stimuli were created using Audacity (version 2.0.3, audacity.sourceforge.net). The tone for the stimuli was created using the Risset Drum tool creating a short percussive sound (Settings: frequency = 1 kHz, decay = 0.1 s, center frequency of noise = 500 Hz, width of noise band = 400 Hz, amount of noise in mix = 25%, normalized amplitude). As a tone shorter than 100 ms could not be produced using this tool, the duration of the tone was modified to 50 ms resulting in a doubling of the frequencies as compared to the original. This tone, or event, sounds like a short ‘woodblock’ and was used for all stimuli (Fig. 1).

The regular training stimulus (S^+ ; see Fig. 2a) was made up of eight isochronous intervals (nine sound events). The total stimulus duration for the training stimuli was 1450 ms, where one single tone lasted 50 ms, and the average IOI duration was 175 ms. The irregular training stimuli (S^-_1 to S^-_4 ; see Fig. 2a) were created using a random number generator for all intervals, except for the first two (which had a fixed duration) and the last interval (which was calculated by subtracting the total duration of the other intervals from the total duration). In choosing the tempo manipulations, we took into account that studies on European starlings and budgerigars showed that songbirds may display little discrimination between stimulus durations in the range of 10–20% of the reference duration (Dooling, 1978; Maier, 1990). Therefore, we excluded a range of 10% on both sides of the average (175 ms) from the irregular IOI range (i.e. resulting in an irregular range varying between 100–157 ms and 193–250 ms), to make the distinction between S^+ and S^- more prominent. Moreover, if the first IOI already differed between the isochronous and irregular stimuli, the zebra finches might use this local feature to distinguish between these stimuli. Since we want the birds to attend to the global feature of the rhythm we wanted them to attend to the full length stimuli. Therefore, to prevent the birds from using the first IOI of the stimuli, we made the first two intervals for the irregular stimulus identical to the IOI of the isochronous stimulus (175 ms).

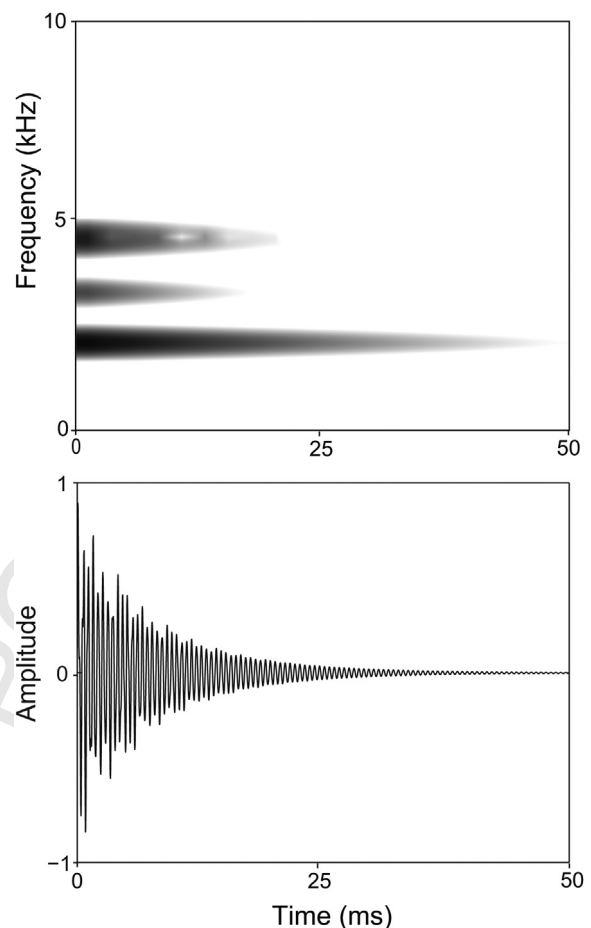


Fig. 1. Acoustic analyses. Spectrogram (top) and waveform (bottom) of the sound event used in all experiments.

Two types of probe stimuli were constructed, one set with tempo manipulations and one set with a manipulation of the total duration. The tempo probes were constructed by scaling the training stimuli with factors 0.75, 0.875, 1.125, and 1.25 (Fig. 2b). This resulted in the new tempos of the isochronous stimuli having an IOI of 131 ms, 153 ms, 199 ms and 219 ms, respectively, for all intervals. The irregular stimuli had an IOI range of 75–119 ms and 144–188 ms for the 0.75 IOI tempo, 88–138 ms and 168–219 ms for the 0.875 IOI tempo, 113–177 ms and 217–281 ms for the 1.125 IOI tempo, 125–197 ms and 241–313 ms for the 1.25 IOI tempo. The average IOI of these new irregular tempos was identical to the IOI of the respective isochronous tempo. The stimuli with the shortest IOI (0.75) thus had the highest tempo. The new tempos had the same number of intervals (and events) and the same tone duration as the training stimuli. The new tempos therefore had a different total stimulus duration, namely 1100 ms, 1275 ms, 1625 ms and 1800 ms respectively. See the Supplementary material for examples of the stimuli. To control for the change in stimulus duration, we also made a new stimulus set with identical average IOI compared to the training stimuli (175 ms), but which had up to two more or fewer events (further indicated as ‘duration controls’). This resulted in 4 new stimuli for both isochronous and irregular, which had 6, 7, 9, and 10 intervals. For the isochronous duration controls we could easily remove 2 events from the original stimulus, but in order to get an identical duration for the irregular stimuli compared to the new tempos, we made new irregular stimuli which resembled the original training stimuli, but with a fixed total stimulus duration (Fig. 2c)

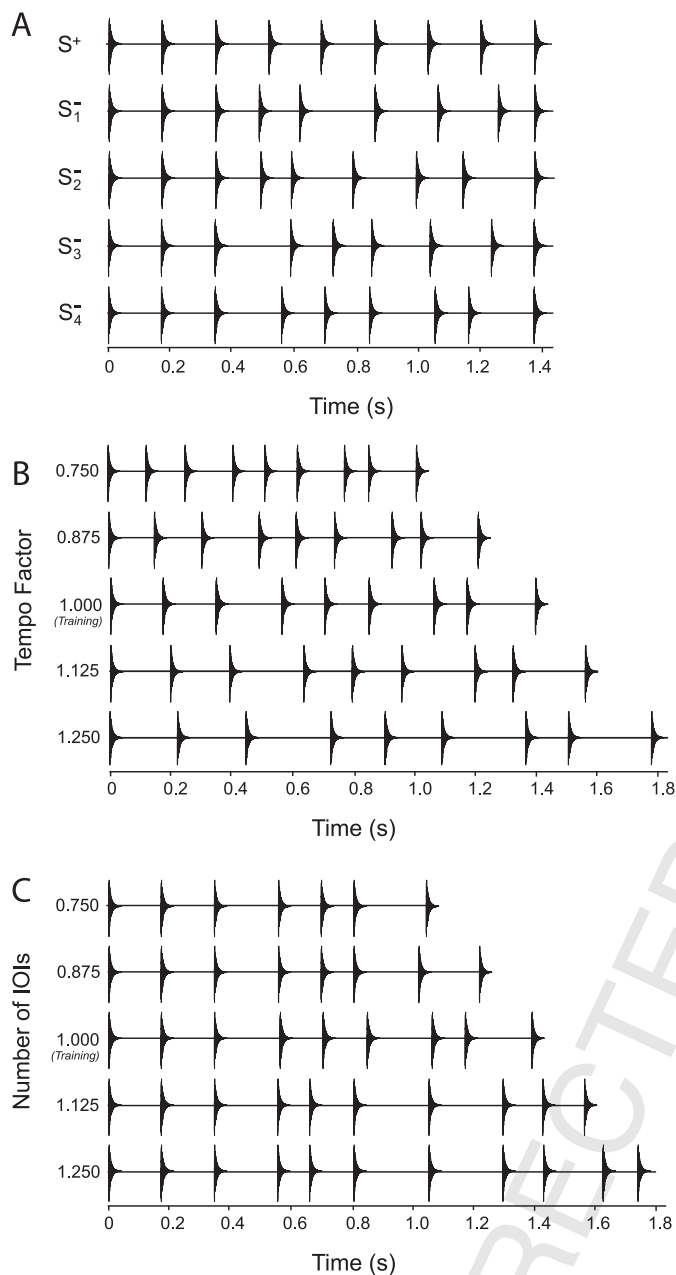


Fig. 2. Stimuli used in Experiment 1. (A) Training stimuli: each bird received the same S^+ and one of the S^- (different for the four birds). (B) Testing stimuli manipulating tempo. (C) Testing stimuli manipulating # of IOIs.

The irregular duration controls were created by first removing excess intervals for the 6 and 7 IOI probes. Removing these intervals led to a discrepancy, Δ , between the actual total duration and the desired total duration. This Δ was then randomly distributed over the remaining intervals excluding the first two, leading to the desired total duration. For the longer irregular duration controls we used the same procedure as with 6 IOIs, with the additional intervals (except the last one) being generated with a random number generator. These duration controls therefore had an identical stimulus duration compared to the new tempos, namely 1100 ms, 1275 ms, 1625 ms and 1800 ms. During testing (probe presentation) all the stimuli described above were presented to the zebra finches in the same test period. The training stimuli constituted 80% of all trials, and remained reinforced. The remaining 20%

the trials constituted all the above described manipulations, both in tempo and in duration.

2.1.5. Statistics

All statistics were performed with the statistical packages for R (CRAN, <http://cran.r-project.org/>) within RStudio (v0.97.449, <http://www.rstudio.com/>). The data, number of go-responses, was analyzed with a binomial logistic regression using a generalized linear mixed model, using the lme4 package (*glmer*). Type of stimulus was a fixed factor, and the individual birds were entered into the model as a random factor. Overdispersion was corrected for by adding a random factor with a different level for each observation. Post-hoc Tukey pairwise analysis was performed using the mult-comp package (*glht*). Both packages are freely available from the R website (<http://cran.r-project.org/>). A p -value of 0.05 or smaller is considered to be statistically significant.

2.2. Results

2.2.1. Training

All birds learned to distinguish the isochronous from the irregular training stimuli (average 9743 trials \pm 2580 SEM, range 4340–16130, $n=4$). The number of trials per day varied among birds, but was on average 610 \pm 70 SEM during training.

2.2.2. Tempo and duration manipulations

Results from this test are shown in Fig. 3. Both isochronous 0.875 and 1.125 did not lead to a significantly different response from the training stimulus, however responses to both isochronous 0.75 and 1.25 were significantly different ($p < 0.01$ for both isochronous 0.75 and isochronous 1.25, Fig. 3a). Moreover, isochronous 0.875 and isochronous 1.125 were the only isochronous stimuli that differed significantly from the irregular training stimulus ($p < 0.01$ for both

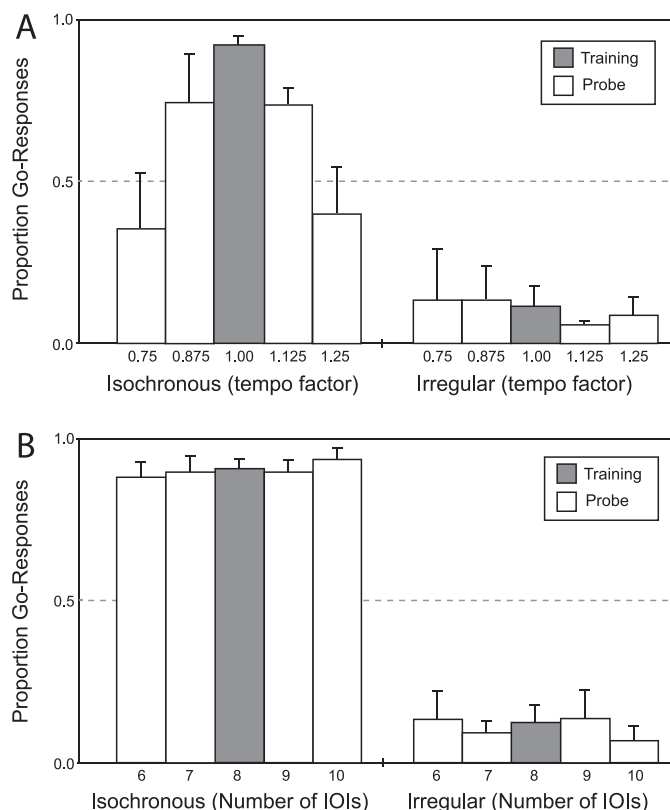


Fig. 3. Results of Experiment 1 ($N=4$). Averaged response probabilities (\pm SEM) to the stimuli for the (A) tempo manipulation and (B) duration controls.

isochronous 0.875 and isochronous 1.125). There was no significant difference in the response to the new irregular tempos compared to the original training irregular tempo.

There was no significant difference between any of the duration controls and their respective training stimulus (Fig. 3b). This indicates that the difference in responses to both isochronous 0.75 and 1.25 cannot be explained by the change in duration.

2.3. Discussion

The finding that the zebra finches were able to discriminate between the two training stimuli with no other cues than the differences in IOI shows they can pay attention to temporal information. This result is in line with the results of Lampen et al. (2014) showing that exposure to a rhythmic or an arrhythmic song resulted in differential ZENK expression in various brain nuclei. However, our finding that the zebra finches hardly generalized to the new isochronous tempos shows that discrimination between two stimuli of which one is regular and the other is not does not imply that the birds are sensitive to ‘regularity’ or ‘irregularity’ as such. Although there was no significant difference between the responses to the isochronous training stimulus and isochronous test stimuli 0.875 and 1.125, the figure suggests that the responses to these stimuli was reduced, but that the small number of birds ($n=4$) resulted in a lack of power to detect a significant difference. Together with the significantly reduced responses to isochronous 0.75 and 1.25, the most likely interpretation of the results is that the birds did not show a categorical perception of isochronous versus irregular, but a generalization around the isochronous training stimulus, showing fewer responses the more a stimulus deviated from this training stimulus. It is thus most likely that the birds had learned to respond to the isochronous training stimulus only and to withhold responses to all stimuli dissimilar from the isochronous training stimulus tempos. The lack of significant differences among the responses to the new irregular tempos might indicate that the birds generalized the irregular training stimulus to the new tempos by perceptual invariance for the rhythm, but a more likely interpretation is that the birds do notice the differences among these stimuli, but do not respond to them due to their dissimilarity from the isochronous stimulus. In other words, the training resulted in the birds showing an excellent discrimination among stimuli, with responding only to stimuli being very similar to the specific isochronous training stimulus.

Considering the results found in starlings (Hulse et al., 1984), where the birds showed perfect generalization over an IOI range of 75–150%, the performance displayed by the zebra finches can thus be considered poor with respect to rhythmic generalization over tempos. Differences between our study and their study, apart from a species difference, may also be due to a difference in training method. The IOI for the isochronous stimulus was rather similar (175 ms here, 200 ms in Hulse et al., 1984), although the tone duration was shorter in our study (50 ms; 100 ms in Hulse et al., 1984). Another difference during training is the larger irregular IOI range used (60–600 ms) in the starling training compared to ours (100–250 ms). Moreover, the stimuli were presented for 4 s (i.e., 20 intervals for the isochronous stimulus) before the starlings were able to respond and the stimulus presentation was continued until the birds actually gave a response. This longer stimulus presentation, in combination with the larger IOI range used, might have made it easier for the birds to perceive the rhythmicity of these stimuli. Finally, the irregular stimuli in the starling study were produced randomly during the experiment, while we trained the birds with one single irregular stimulus. It could be that the greater diversity of irregular stimuli facilitated formation of a general rule which resulted in generalization of the rhythmic patterns over different tempos.

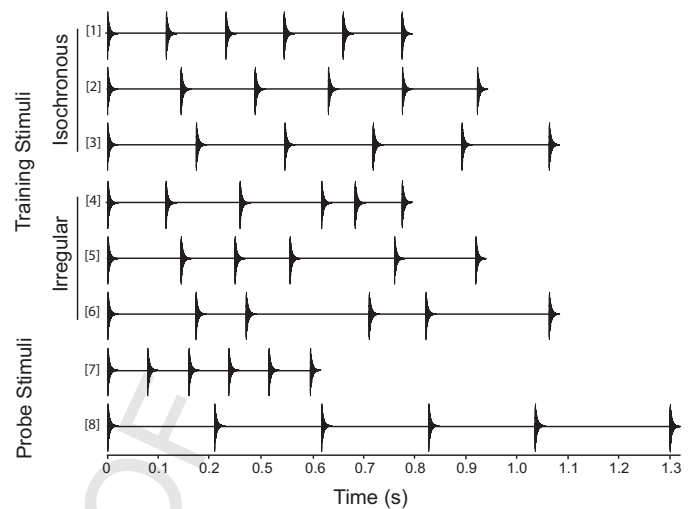


Fig. 4. Stimuli used in Experiment 2. Training stimuli: [1] Isochronous 0.80, [2] Isochronous 1.00, [3] Isochronous 1.20, [4] Irregular 0.80, [5] Irregular 1.00, [6] Irregular 1.20. Probes: [7] Isochronous 0.55, [8] Isochronous 1.45. All sound files of this experiment are presented as supplementary material.

Since the birds did not respond to the tempo manipulations of the isochronous stimulus in the same way as they did to the training stimulus, we can conclude that the birds did not use the regularity or the interval ratio to make the distinction. They must have used another feature to arrive at the excellent performance shown in the training, most likely the absolute duration of (some of) the intervals.

3. Experiment 2: Multiple training stimuli

Failure to distinguish the isochronous from the irregular stimulus during the test phase could be due to using a single regular and irregular stimulus, which may have prevented the birds from learning to use the global feature of regularity to distinguish the training stimuli. One of the major differences between our methods and those used in the starling experiment (Hulse et al., 1984) was that the starlings received multiple stimuli of the same categories, while our zebra finches only received one of each. In this second experiment we therefore trained a new group of zebra finches with different rhythms and different tempos, making it harder for the birds to solely use the absolute interval duration as a cue, and to stimulate them to attend to higher order information such as the presence or absence of regularity.

In this experiment, we presented birds with three stimuli per category during training. These stimuli had an average IOI ratio of 0.80, 1.00, and 1.20 of 175 ms, i.e., a duration of 140, 175, and 210 ms. We also constructed three different irregular rhythms, each of which had both a different tempo and a different rhythm (Fig. 4 – see Supplementary data).

3.1. Methods

3.1.1. Animals

Four new birds (2 female and 2 male) from our breeding colony were trained and tested in individual operant conditioning chambers using the same go/no go procedure as for Experiment 1. The birds were naive to the setup and training.

3.1.2. Stimuli

Instead of 8 intervals, the stimuli used during this experiment contained only 5 intervals (thus 6 events). Moreover, we only kept the first interval identical between the isochronous and its respective irregular training stimulus. This meant that the birds had 4

intervals on which they could base the distinction. The training stimuli had a total duration of 750, 925, and 1100 ms.

In order to test whether the birds were using the regularity to make the distinction after having had multiple stimuli of the same category during training, we presented the birds with 2 new isochronous probes, one with an IOI manipulation with a factor of 0.55 and one with a factor of 1.45 of the average IOI (175 ms). These stimuli therefore had an IOI of 96 and 254 ms (Fig. 4), leading to a total duration of 531 and 1319 ms. If the birds were using the regularity in the stimuli to make the distinction, we expected them to respond similarly to the probes as to the isochronous training stimuli.

The stimuli were created using Audacity (version 2.0.3, audacity.sourceforge.net) using the same tone as used in the previous experiment (see Fig. 1). First, the irregular stimuli and the isochronous stimulus with an average IOI of 175 were created. The irregular stimuli were created using a random number generator. The last interval (5th) was calculated by subtracting the total duration of interval 1–4 from the total interval duration (875 ms). All different tempos were constructed based on these stimuli with an average IOI of 175 ms by multiplying the IOI with the respective manipulation factor. The test procedure was identical to Experiment 1, with 80% of the stimuli being training stimuli and 20% of the stimuli being probes during testing.

3.1.3. Statistics

Statistics are identical to Experiment 1. For statistics on the probe experiment, both the isochronous and the irregular training stimuli were grouped into the two training categories during analyses, since grouping significantly improved the models. Despite the fact that there were significant differences between the irregular training stimuli (see below), grouping did not change the results and the subsequent interpretation.

3.2. Results

3.2.1. Training

All four birds learned to distinguish the isochronous from the irregular training stimuli (average 19256 trials \pm 9542 SEM, range 5732–47544, $n=4$). The number of trials per day varied among birds, but was on average 644 \pm 134 SEM during training. Responses to the training results are depicted in Fig. 5. No significant differences in responses were found among the isochronous training stimuli. The irregular 1.20 training stimulus resulted in significantly fewer responses than the remaining irregular training stimuli ($p < 0.001$ for irregular 1.00, $p = 0.018$ for irregular 0.80). There was a trend toward a significant difference between irregular 1.00 and irregular 0.80 ($p = 0.061$). These results were also visible in the

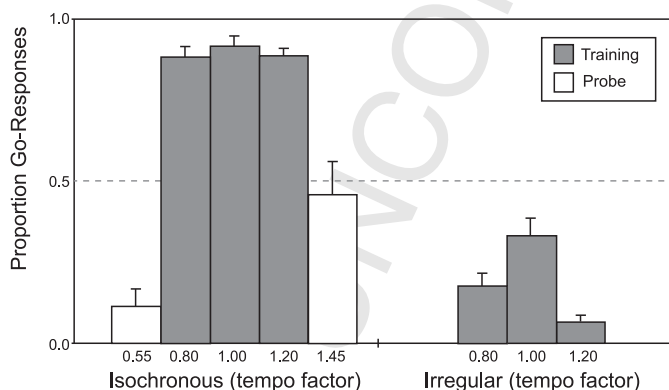


Fig. 5. Results of Experiment 2 ($N=4$). Averaged response probabilities (\pm SEM) to the stimuli.

learning curves of all the birds, showing that withholding responses to irregular 1.20 was learned fastest by all the birds, whereas withholding responses to irregular 1.00 appeared to be hardest to learn for all the birds (data not shown).

3.2.2. Tempo manipulations

Responses to the probes are also presented in Fig. 5. The birds responded significantly less to isochronous 1.45 compared to the isochronous training stimuli ($p < 0.001$), however the birds still responded more to this stimulus than to the irregular training stimuli ($p < 0.001$). Birds also responded significantly less to isochronous 0.55 as compared to the isochronous training stimuli ($p < 0.001$), but there was no significant difference between isochronous 0.55 and the irregular training stimuli.

3.3. Discussion

The zebra finches once again did not display tempo generalization over the isochronous stimuli. Despite the fact that the training phase encouraged the birds to attend to the regularity (as an overall quality of the S^+ stimuli), the birds clearly did not make this generalization. This is was already reflected in the training itself. All birds had least difficulty with learning irregular 1.20, and greatest difficulty with irregular 1.00. This indicates that the birds seem to learn the stimuli independently, with some stimuli apparently being easier to learn than others, meaning the birds did not seem to learn a general rule (such as regularity).

The fact that the birds had the greatest difficulty with irregular 1.00 suggests that the birds were using the absolute interval information, regardless of it being a lot more difficult with multiple tempos during training. The IOI's for this stimulus are closer in absolute values to those present in the isochronous stimuli, in contrast to the long intervals for irregular 1.20 (largest interval 293 ms) and short intervals for irregular 0.80 (shortest interval 80 ms), which are not present in any of the isochronous training stimuli (140, 175, and 210 ms). Since these intervals are unique for those two irregular stimuli, it might have been easier for the birds to utilize these unique intervals to distinguish the stimuli.

4. Experiment 3: humans

The aim of this experiment was to assess whether humans were able (without explicit instruction) to detect and generalize the regularity versus irregularity distinction using a similar set of stimuli used in the experiments with zebra finches.

4.1. Methods

4.1.1. Participants

Eleven human volunteers (7 male, 4 female; age 29.3 \pm 3.7 years) participated in this experiment. None of the participants had any musical experience beyond the standard Dutch education curriculum. They received no compensation for their participation.

4.1.2. Test procedure

The participants performed the experiment on a computer while being comfortably seated in a quiet environment. During the experiment, they wore headphones (Marshall Major 50 FX) calibrated to an output of 70 dB (SPL meter, RION NL 15, RION) at the ears. The experiment was written and run with Processing (v2.0b8; <http://processing.org/>). A single trial started with a white screen with a speaker icon in the middle. Participants could self-initiate a trial by clicking on the icon with the mouse. Consequently, a stimulus was played during which the screen was white. After stimulus presentation two colored squares appeared on the screen, one green and one red, one on the left and one on the right. Before the

experiment, the participants were only given the instruction to ‘listen to the sound stimuli’ and to ‘click on the colored squares using the mouse’. We gave the participants no further instructions, thus making it comparable to the zebra finch experiments. The position of the colors was randomized between participants, but constant within participants, with one color linked to the S^+ and the other to the S^- . The participants had 5 s to respond by clicking one of the squares using the mouse, after which they proceeded to the next trial. If the participants did not react within 5 s, the trial was terminated and participants proceeded to the next trial.

The experiment consisted of three phases; the training phase, the pre-testing phase, and the test. During the training phase, two training stimuli were presented in random order. These training stimuli were the same as in Experiment 1 (i.e., the isochronous stimulus and irregular stimulus with an average IOI of 175 ms). However, in this experiment the participants received one out of two possible irregular stimuli: S_2^- or S_3^- (see Fig. 2a). During training, participants received visual and auditory feedback after each trial; a happy smiley accompanied by a “ding” sound for a correct response, an angry smiley accompanied by the “attack” sound for an incorrect response, and a “confused” smiley for no response. Once the participants reached the criterion of 75% of the trials correct (over 20 trials), they proceeded to the next phase. Training lasted as long as the participants needed to reach the criterion, with a minimum of 20 trials. In short: the participants were required to give a green response to the isochronous stimulus and a red response for the irregular stimulus, but were not informed about this beforehand.

During the second phase (pre-testing), the participants no longer received feedback after each trial. This phase was intended to make the participants comfortable with the absence of feedback. Ten trials had to be performed with the same stimuli as during training, meaning they received 5 trials per stimulus.

The third phase consisted of testing, again without any post trial feedback. Stimuli during these tests are identical to the stimuli used Experiment 1 (i.e., participants received all 16 different manipulations and the training stimuli during the test). Each stimulus was presented five times during the tests. The minimum duration of the total experiment was about 15 min, and lasted as long as required depending on performance during the training phase. After the experiment, the participants were asked what cues they used to categorize the different stimuli.

4.1.3. Statistics

We took the number of green responses (hereafter referred to as go-responses) as the index for performance. During tests, all participants responded on every trial, meaning that they always responded by either clicking the green or the red square on the screen. Statistics were performed identical to the statistics performed during Experiment 1 (see 2.1.5. Statistics), with the exception that there was no overdispersion, which therefore did not require correction.

4.2. Results

Once participants understood the task, training proceeded quickly. The training phase was finished after on average $34.5 (\pm 9.0)$ SEM) trials. The overall results of this experiment are presented in Fig. 6. No significant differences were found between any of the new tempos and the training stimuli, both for the isochronous and irregular stimuli (Fig. 6a). The same holds for the duration controls and the training stimuli (Fig. 6b). The post-experiment questionnaire revealed that the participants applied different strategies in solving the task. While a majority ($n=6$) reported to have listened for the regularity of the rhythm, some listened for syncopations ($n=2$), “speeding up of the ticks within the rhythm” ($n=1$), or lis-

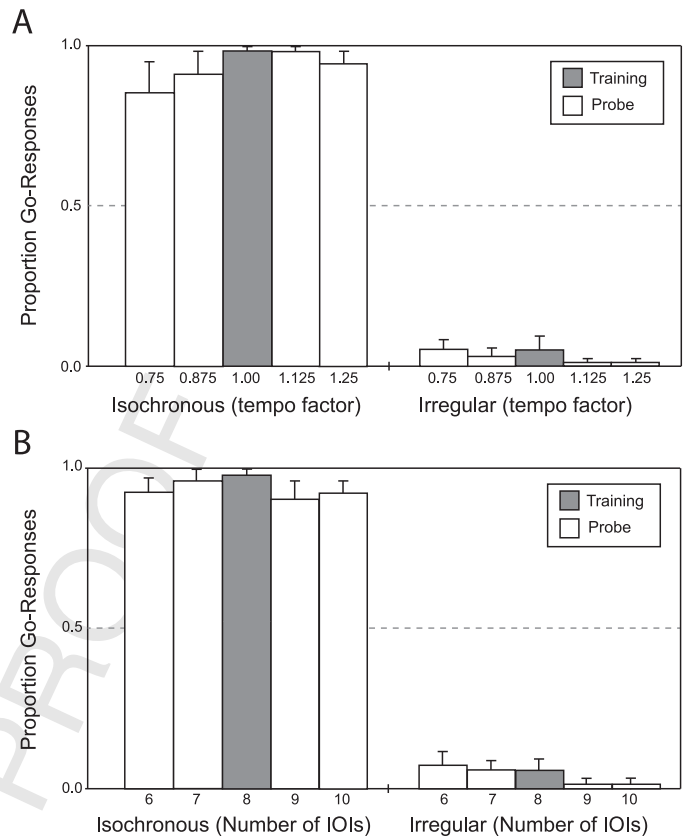


Fig. 6. Results of Experiment 3 ($N = 12$). Averaged response probabilities (\pm SEM) to the stimuli for the (A) tempo manipulation and (B) duration controls.

tened for a difference in frequency of tones in the stimuli ($n = 1$). The latter is peculiar, since all elements had identical frequencies. One participant was unable to explain what he had done. Nevertheless, the performance of these two participants was excellent.

The main difference between the humans and the zebra finches was that humans categorized the stimuli based on being regular or not. To exclude that humans responded similarly to all isochronous stimuli because they could not detect the differences among them, we ran an additional test in which another 12 participants were asked whether or not a tempo difference was present between the 1.0 and each of the other isochronous stimuli as well as whether two identical isochronous showed a difference or not. The participants noted a difference between the isochronous 1.0 and isochronous 0.75, 0.875, 1.125 and 1.25, in, respectively, 100, 93, 61, and 97% of the trials. Two identical isochronous stimuli were correctly scored as identical in 93% or more of the trials. This confirms that humans categorized the isochronous stimuli based on being regular, and not because they failed to detect differences among the isochronous stimuli.

4.3. Discussion

Based on these results, we conclude that humans do show perceptual invariance over different tempos for the rhythmic stimuli used in these experiments, using the interval ratios when listening to these stimuli. It appears that this task was not particularly difficult for humans, since the training phase was relatively short. Nevertheless, the strategy that the participants chose for this apparently simple task can be different and several different listening strategies were reported. Despite these differences, all strategies were based on interval ratio. Although only about half of the participants made conscious use of the regularity of the stimuli, they

all showed tempo generalization, while the zebra finches did not. The relative time information present in the stimuli, which effectively is the basis for tempo generalization, is a requirement for regularity detection as implicated in beat induction.

It seems that zebra finches and humans have a different strategy in dealing with these simple rhythms, with zebra finches showing a preference for using the absolute time information, while the human participants tend to use the relative time information present in these stimuli.

5. General discussion

Our results show that zebra finches can discriminate between a regular and an irregular stimulus. However, our experiments show that this discrimination is not based on distinguishing regularity from irregularity as such. The zebra finches did not use the relative time information (i.e., interval ratios instead of absolute interval durations) to make the distinction between the isochronous and irregular stimuli, but instead seem to focus on absolute differences in specific inter-stimulus intervals. By contrast, the human participants did use relative information, and judged the differences on the basis of the presence (or absence) of regularity.

However these results need not mean that zebra finches are unable to perceive similarities among stimuli changed in tempo. Nagel et al. (2010) demonstrated that zebra finches are able to maintain discrimination between two songs across a range of tempo changes. Generalization was realized over a greater range than presented during our experiment, namely 61–164%, even though there was some decline in generalization with differences greater than 25%. We suggest the difference between the results by Nagel et al. (2010) and ours is most likely due to the nature of the stimuli: regularly spaced beats versus natural songs. Not only is song an ecologically relevant stimulus for zebra finches, their song is also acoustically richer than the stimuli used in the current experiments (i.e., sequences of identical pulses). It could well be that the richness of the stimuli (timbre, pitch and amplitude variation among the elements of a song) is important in establishing regularity detection. Using more complex auditory stimuli, such as songs or artificial stimuli with pitch and amplitude variation, might make that the birds pay more attention to the stimulus as a whole, instead of attending to local detail, such as the length of certain intervals.

Considering the discrepancies between our study and that of Nagel et al. (2010), we cannot simply conclude that zebra finches are unable to detect regularity. It is possible that our stimuli were unsuited for our purpose, and that there are other stimuli that might trigger the zebra finches to attend to the relative information and regularity. One line of further research might be to examine whether adding several prosodic cues (pitch, duration, amplitude; cf. Spierings and ten Cate, 2014), or ‘enriching’ the complexity of the stimulus in other ways, in addition to manipulating temporal information, might help the zebra finches to generalize over tempos.

Our results also differ markedly from those obtained by Hulse et al. (1984) in starlings. When trained in a go/no go task with a single isochronous stimulus and a variable irregular one, the starlings readily transferred the discrimination to faster or slower isochronous stimuli. Although methodological differences might underlie the differences in outcome (see Section 2.3), it is remarkable that even when trained with three isochronous stimuli simultaneously, the zebra finches did not show the transfer. At the same time, the zebra finches were able to discriminate isochronous and irregular training stimuli, an ability that Haggmann and Cook (2010) could not demonstrate for pigeons. So, taken together the results of these three studies may also indicate the existence of

more fundamental species differences in perceiving regularities in tempo, calling for further studies with these and other species to examine the causes of such differences.

Regularity detection can be seen as a necessary (though not sufficient) condition for beat induction. Beat induction has been suggested to be linked with vocal learning (Patel et al., 2009; Schachner et al., 2009). If it is true that zebra finches are unable to show regularity detection, this would mean that not all vocal learners would have a potential for demonstrating beat induction. In this respect it may be relevant that the only bird species that thus far have shown any evidence of beat induction are members of the parrot family—no such evidence exists for songbirds or other bird species (see also Hoeschele et al. (2015), for a discussion on the relationship between vocal learning and beat induction).

Finally, although we found no evidence for regularity detection in zebra finches, it should be noted that the birds were very well able to discriminate the various stimuli. If they did so, as we expect, by paying attention to the durations of specific IOI's, this would be a remarkable achievement. This feature can only be used if the birds could assess and memorize the exact durations of at least one, but possibly more, of the intervals 2–5 (the first interval was identical for isochronous and irregular stimuli) for (in Experiment 2) at least the three isochronous and possibly, but not necessarily, the three irregular stimuli simultaneously. While many animals are able to memorize stimulus intervals in experiments, these generally concern single long (seconds rather than ms) intervals (e.g., Church, 2012) and in the current experiment the critical brief intervals are embedded among other ones. We are not aware of any study demonstrating or examining such abilities. From our human perspective, this seems a much more complex criterion to use than attending to the regularity of the stimuli.

Acknowledgements

The second author (H.H.) is supported by the Distinguished Lorentz Fellowship and Prize 2013/14 granted by the Lorentz Center for the Sciences and the Netherlands Institute for Advanced Study in the Humanities and Social Sciences (NIAS).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.beproc.2015.02.018>.

References

- Cook, P., Rouse, A., Wilson, M., Reichmuth, C., 2013. A California sea lion (*Zalophus californianus*) can keep the beat: motor entrainment to rhythmic auditory stimuli in a non vocal mimic. *J. Comp. Psychol.* 127, 412–427, <http://dx.doi.org/10.1037/a0032345>.
- Doolling, R.J., 1978. Auditory duration discrimination in the parakeet (*Melospittacus undulatus*). *J. Acoust. Soc. Am.* 63, 1640, <http://dx.doi.org/10.1121/1.381865>.
- Fitch, W.T., 2009. Biology of music: another one bites the dust. *Curr. Biol.* 19, R403–R404, <http://dx.doi.org/10.1016/j.cub.2009.04.004>.
- Fitch, W.T., 2013. Rhythmic cognition in humans and animals: distinguishing meter and pulse perception. *Front. Syst. Neurosci.* 7, 68, <http://dx.doi.org/10.3389/fnsys.2013.00068>.
- Haesler, S., Wada, K., Nshdejan, A., Morrisey, E.E., Lints, T., Jarvis, E.D., Scharff, C., 2004. FoxP2 expression in avian vocal learners and non-learners. *J. Neurosci.* 24, 3164–3175, <http://dx.doi.org/10.1523/JNEUROSCI.4369-03.2004>.
- Haggmann, C.E., Cook, R.G., 2010. Testing meter, rhythm, and tempo discriminations in pigeons. *Behav. Processes.* 85, 99–110, <http://dx.doi.org/10.1016/j.beproc.2010.06.015>.
- Hasegawa, A., Okanoya, K., Hasegawa, T., Seki, Y., 2011. Rhythmic synchronization tapping to an audio–visual metronome in budgerigars. *Sci. Rep.* 1, 1–8, <http://dx.doi.org/10.1038/srep00120>.
- Hoeschele, M., Merchant, H., Kikuchi, Y., Hattori, Y., ten Cate, C., 2015. Comparative studies on music perception: bridging the gap between constrained experiments and natural behavior in the search for musicality. *Phil. Trans. R. Soc. B.* 370, 20140094, <http://dx.doi.org/10.1098/rstb.2014.0094>.

- 753 Honing, H., 2012. Without it no music: beat induction as a fundamental musical
754 trait. *Ann. N. Y. Acad. Sci.* 1252, 85–91,
755 <http://dx.doi.org/10.1111/j.1749-6632.2011.06402.x>.
- 756 Honing, H., Ploeger, A., 2012. Cognition and the evolution of music: Pitfalls and
757 prospect. *Top. Cogn. Sci.* 4, 513–524,
758 <http://dx.doi.org/10.1111/j.1756-8765.2012.01210.x>.
- 759 Honing, H., ten Cate, C., Peretz, I., Trehub, S.E., 2015. Without it no music:
760 cognition, biology and evolution of musicality. *Phil. Trans. R. Soc. B.* 370,
761 20140088, <http://dx.doi.org/10.1098/rstb.2014.0088>.
- 762 Hulse, S.H., Humpal, J., Cynx, J., 1984. Discrimination and generalization of
763 rhythmic and arrhythmic sound patterns by European starlings (*Sturnus*
764 *vulgaris*). *Music Percept.* 1, 442–464, <http://dx.doi.org/10.2307/40285272>.
- 765 Jarvis, E.D., 2007. Neural systems for vocal learning in birds and humans: a
766 synopsis. *J. Ornithol.* 148, S35–S44,
767 <http://dx.doi.org/10.1007/s10336-007-0243-0>.
- 768 Lampen, J., Jones, K., McAuley, J.D., Chang, S.E., Wad, J., 2014. Arrhythmic song
769 exposure increases ZENK expression in auditory cortical areas and nucleus
770 Taeniae of the adult zebra finch. *PLoS One* 9, e108841,
771 <http://dx.doi.org/10.1371/journal.pone.0108841>.
- 772 Lohr, B., Dooling, R.J., 1998. Detection of changes in timbre and harmonicity in
773 complex sounds by zebra finches (*Taeniopygia guttata*) and budgerigars
774 (*Melopsittacus undulatus*). *J. Comp. Psychol.* 112, 36–47,
775 <http://dx.doi.org/10.1037/0735-7036.112.1.36>.
- 776 Maier, E.H., 1990. Auditory duration discrimination in the European starling
777 (*Sturnus vulgaris*). *J. Acoust. Soc. Am.* 88, 616,
778 <http://dx.doi.org/10.1121/1.399765>.
- 779 Merchant, H., Honing, H., 2014. Are non-human primates capable of rhythmic
780 entrainment? Evidence for the gradual audiomotor evolution hypothesis.
781 *Front. Neurosci.* 7, 274, <http://dx.doi.org/10.3389/fnins.2013.00274>.
- 782 Nagel, K.I., Mclendon, H.M., Doupe, A.J., 2010. Differential influence of frequency,
783 timing, and intensity cues in a complex acoustic categorization task. *J.*
784 *Neurophysiol.* 104, 1426–1437, <http://dx.doi.org/10.1152/jn.00028.2010>.
- 785 Okanoya, K., Dooling, R.J., 1987. Hearing in passerine and psittacine birds: a
786 comparative study of absolute and masked auditory thresholds. *J. Comp.*
787 *Psychol.* 101, 7–15, <http://dx.doi.org/10.1037/0735-7036.101.1.7>.
- 788 Patel, A.D., 2006. Musical rhythm, linguistic rhythm, and human evolution. *Music*
789 *Percept.* 24, 99–104, <http://dx.doi.org/10.1525/mp.2006.24.1.99>.
- Patel, A.D., 2008. *Music, Language, and the Brain*. Oxford University Press, Oxford.
- Patel, A.D., Iversen, J.R., Bregman, M.R., Schulz, I., 2009. Studying synchronization
790 to a musical beat in nonhuman animals. *Ann. N. Y. Acad. Sci.* 1169, 459–469,
791 <http://dx.doi.org/10.1111/j.1749-6632.2009.04581.x>.
- Peretz, I., Coltheart, M., 2003. Modularity of music processing. *Nat. Neurosci.* 6,
792 688–691, <http://dx.doi.org/10.1038/nn1083>.
- Schachner, A., Brady, T.F., Pepperberg, I.M., Hauser, M.D., 2009. Spontaneous motor
793 entrainment to music in multiple vocal mimicking species. *Curr. Biol.* 19,
794 831–836, <http://dx.doi.org/10.1016/j.cub.2009.03.061>.
- Slabbekoorn, H., ten Cate, C., 1999. Collared dove responses to playback: slaves to
795 the rhythm. *Ethology* 105, 377–391,
796 <http://dx.doi.org/10.1046/j.1439-0310.1999.00420.x>.
- Spierings, M.J., ten Cate, C., 2014. Zebra finches are sensitive to prosodic features of
797 human speech. *Proc. R. Soc. B.* 28, 1, <http://dx.doi.org/10.1098/rspb.2014.0480>.
- Trehub, S.E., 2003. The developmental origins of musicality. *Nat. Neurosci.* 6,
798 669–673, <http://dx.doi.org/10.1038/nn1084>.
- van Heijningen, C.A.A., Chen, J., van Laatum, I., van der Hulst, B., ten Cate, C., 2013.
799 Rule learning by zebra finches in an artificial grammar learning task: which
800 rule? *Anim. Cogn.* 16, 165–175, <http://dx.doi.org/10.1007/s10071-012-0559-x>.
- van Heijningen, C.A.A., de Visser, J., Zuidema, W., ten Cate, C., 2009. Simple rules
801 can explain discrimination of putative recursive syntactic structures by a
802 songbird species. *Proc. Natl. Acad. Sci. U. S. A.* 106, 20538–20543,
803 <http://dx.doi.org/10.1073/pnas.0908113106>.
- Verzijden, M.N., Etman, E., van Heijningen, C., van der Linden, M., ten Cate, C., 2007.
804 Song discrimination learning in zebra finches induces highly divergent
805 responses to novel songs. *Proc. R. Soc. B* 274, 295–301,
806 <http://dx.doi.org/10.1098/rspb.2006.3728>.
- Wallin, N.L., Merker, B., Brown, S. (Eds.), 2000. *The Origins of Music*. MIT Press,
807 Cambridge, MA.
- Weisman, R., Njegovan, M., Sturdy, C., Phillmore, L., Coyle, J., Mewhort, D., 1998.
808 Frequency-range discriminations: special and general abilities in zebra finches
809 (*Taeniopygia guttata*) and humans (*Homo sapiens*). *J. Comp. Psychol.* 112,
810 244–258, <http://dx.doi.org/10.1037/0735-7036.112.3.244>.
- Winkler, I., Háden, G.P., Ladinig, O., Sziller, I., Honing, H., 2009. Newborn infants
811 detect the beat in music. *Proc. Natl. Acad. Sci. U. S. A.* 106, 2468–2471,
812 <http://dx.doi.org/10.1073/pnas.0809035106>.