



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



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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.

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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.

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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 DeLuxe 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

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