

Discrimination of Temporal Regularity in Rats (*Rattus norvegicus*) and Humans (*Homo sapiens*)

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The perception of temporal regularities is essential to synchronize to music and dance. Here, we explore the detection of isochrony in two mammal species. We trained rats (*Rattus norvegicus*) and humans (*Homo sapiens*) to discriminate sound sequences with regular intervals from sound sequences with irregular intervals using a go/no-go paradigm. We used four different tempi in the training sessions and two new tempi in the tests. We found that both rats and humans responded more to the novel regular test sequences than to the novel irregular test sequences. Differently from previous studies with birds, rats seem to have focused on the relative duration of the sounds, which means that they paid attention to global features defining the regularity of the sequences. In sum, this study suggests that detecting temporal regularities in sequences of sounds may have ancient evolutionary roots and could rely on timing mechanisms present in distantly related mammals.

Keywords: beat perception, isochrony, tempo, rat, music evolution

Rhythm is a fundamental feature of music, dance, and language. It lies at the root of the human universal of gathering in groups to sing and dance following a shared beat (Merker, Madison, & Eckerdal, 2009). The extraction of temporal regularities from acoustical patterns is fundamental to organize the motifs of a song, the gestures of a dance, or the syllables of a sentence. These abilities rely on similar timing mechanisms that may have evolved interacting with each other to finally allow for our current rhythmic cognition (Fitch, 2013; Patel, 2006, 2010; Ravignani & Madison, 2017). Interestingly, the detection of temporal regularities is not restricted to humans, suggesting that similar evolutionary pressures may have paved the way to rhythmic cognition in other species (Fitch, 2006; Kotz, Ravignani, & Fitch, 2018; Ravignani et al. 2013). Here, we explore how two distant mammal species discriminate regular auditory sequences from irregular ones while controlling for the global timing features of beat, tempo, and relative durations.

The present study focuses on the detection of regularity (i.e., isochrony): the ability to identify a constant interevent interval in a sequence of events presented regularly (Geiser, Walker, & Bendor, 2014). The detection of isochrony seems to be fundamental for sensorimotor synchronization across individuals and may have appeared long ago in the animal lineage (Ravignani & Madison, 2017; Wilson & Cook, 2016). Detecting temporal regularity may be one of the first steps to inferring the beat. Although isochrony refers to the physical property of equal intervals in time, the beat refers to the cognitive construct of periodic events in time that are not always perceptually present in the signal (Thaut, 2013). Two timing mechanisms could account for the perception of isochrony (Schulze, 1978). The first would be an interval timer that compares the intervals between the events, either adjacently or by a memory trace of averaged intervals (Keele, Nicoletti, Ivry, & Pokorny, 1989; Madison, 2004; Madison & Delignières, 2009). The second would be a beat-based timer that establishes an endogenous beat by predicting the event, possibly due to neural oscillators that resonate to the external stimulus (Large & Snyder, 2009) and engage auditory and motor regions of the brain (Merchant, Grahn, Trainor, Rohrmeier, & Fitch, 2015; Patel & Iversen, 2014).

Whether and how beat perception is linked to the synchronized behavior across species has extensively been debated during the past decade, from the chorus of crickets and the antisynchrony of crabs to the synchronized blinking of fireflies (Kotz et al., 2018; Ravignani, 2015; Wilson & Cook, 2016). The vocal learning beat perception and synchronization hypothesis (Patel, 2006; Patel, Iversen, Bregman, & Schulz, 2009; Schachner, Brady, Pepperberg, & Hauser, 2009) proposes that only vocal learning species can extract and entrain to a periodic pulse. Vocal learning is the ability to imitate and modify vocalizations learned from other individuals (Marler, 1976), thanks to specific neural connections between auditory and motor regions of the brain (Jarvis, 2006, 2007; Patel

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& Iversen, 2014; Petkov & Jarvis, 2012). However, current animal studies have observed beat entrainment in nonvocal learners (Wilson & Cook, 2016). A sea lion (*Zalophus californianus*) was trained to bob her head to the beat of a song (Cook, Rouse, Wilson, & Reichmuth, 2013), a bonobo (*Pan paniscus*) was found to spontaneously drum in interaction with an experimenter (Large & Gray, 2015), and a chimpanzee (*Pan troglodytes*) and three rhesus monkeys (*Macaca mulatta*) were trained to finger-tap with a metronome (Hattori, Tomonaga, & Matsuzawa, 2013; Zarco, Merchant, Prado, & Mendez, 2009). The reported findings make the comparison of vocal learning and nonvocal learning species a very promising enterprise because it may elucidate up to what point this ability could be necessary to discriminate the basic properties of the acoustic rhythms.

Previous research with birds has explored the discrimination of regularity in rhythmic patterns. These studies suggest that (a) pigeons (*Columba livia*) are unable to discriminate regular sounds from irregular sounds (Hagmann & Cook, 2010), (b) zebra finches (*Taeniopygia guttata*) and budgerigars (*Melopsittacus undulatus*) are able to discriminate regular and irregular stimuli by focusing more on absolute/local than on relative/global features (Spierings & ten Cate, 2016; ten Cate, Spierings, Hubert, & Honing, 2016; van der Aa, Honing, & ten Cate, 2015), and (c) starlings (*Sturnus vulgaris*) and jackdaws (*Coloeus monedula*) could transfer regularity discrimination to stimuli at faster or slower tempi by focusing more on relative/global than on absolute/local features (Hulse, Humpal, & Cynx, 1984; Reinert, 1965). Interestingly, budgerigars can adjust their self-paced pecking behavior toward an external metronome (Seki & Tomyta, 2019). These studies reveal differences regarding the degree of discrimination across bird species and the auditory features used to detect regularity.

Studies using electroencephalographic methods have hinted at regularity detection in rodents. In one study, Herry et al. (2007) presented C57BL/6J mice (*Mus musculus*) with 2-min sequences of 5-kHz short sounds, either regular (inter-onset intervals [IOI] = 200 ms) or irregular, and found that the jittered sequences elicited more activity in the amygdala. In another study, Rajendran, Harper, Garcia-Lazaro, Lesica, and Schnupp (2017) tested anesthetized gerbils (*Jerbus petiti*) with nine different rhythmic sequences and found distinct evoked firing rates for on-beat and off-beat positions of the sounds. In a pharmacological study with rats, Jongasma, Coenen, and Van Rijn (2002) recorded the omission evoked potentials of male Wistar rats and found that the random omission of 10% of the 11-kHz pure tone-pip stimuli elicited a late-latency positive wave in the isochronous condition (inter-stimulus interval of 3 s) but not in the jittered condition (inter-stimulus interval varying from 2.5 to 3.5 s). Although these three rodent studies reveal neural sensitivity to isochrony and the beat, little is known regarding rats' behavioral discriminatory responses to regular and irregular sound sequences.

In sum, here we test two kinds of mammals: a nonvocal learning species, *Rattus norvegicus*, and a vocal learning species, *Homo sapiens*. We compare the behavioral responses of rats and humans on their task to discriminate sequences of regular sounds from sequences of irregular sounds. Based on the previously mentioned studies in birds and nonvocal learner mammals, we hypothesize that detecting regularity might not depend on vocal learning abilities and that both rats and humans would discriminate regular from irregular stimuli. In fact, the detection of acoustic regularity

could be linked to the awareness of an automatic low-level process, in which trains of constant-rate sounds elicit auditory steady-state responses in the brain that are phase-locked to the amplitude of the signal (Will & Berg, 2007). This neural entrainment to the amplitude-modulated acoustic signals seems to be also present in rats (Conti, Santarelli, Grassi, Ottaviani, & Azzena, 1999; Prado-Gutierrez et al. 2015). Therefore, the lack of difference between the responses of rats and humans may imply that both species are able of detecting regularity regardless of the involvement of any vocal learning ability.

Experiment With Rats

Method

Subjects. Subjects were 32 female Long-Evans rats of 4 months of age, caged in pairs within a pathogen-free room, and exposed to a light–dark cycle of 12hr/12hr. Rats were food-deprived until they reached 85% to 90% of their free-feeding weight. They had access to water ad libitum. Food was always administered after each training session.

Stimuli. Stimuli were sequences of 12 tones that we synthesized with MATLAB (v.2013, The MathWorks, Natick, MA). Each tone consisted of consisted of a pure sine wave with one of five different fundamental frequencies (f), and its first and second overtones ($2f$ and $3f$). We applied 10 ms of cosine ramps to fade in and fade out the auditory signal. The 12 tones of each sequence had always the same pitch and duration. To create more variability in the training and test stimuli, we used five different pitches for each tempo. The pitches were F5 (698.5 Hz), A5 (880 Hz), C6 (1,046.5 Hz), E6 (1,318.5 Hz), and G6 (1,568 Hz). Adding variability to the training stimuli might help the listeners to focus on the underlying general regularity (e.g., Gómez, 2002).

There were two kinds of sequences: regular and irregular. The regular sequences had isochronous IOIs between the sounds. The irregular sequences were created by jittering the onset of the sounds of the regular sequences. Each sound event was moved forward or backward in time relative to the first and last events, whose interval remained constant (Figure 1). Thus, we preserved the number of the sounds and the total duration of the stimulus (i.e., the time interval between the onset of the first sound and the ending of the 12th sound was the same for regular and irregular sequences). We moved the 10 central sounds by shifting them in relation to their canonical position by a certain percentage of the IOI: ± 25 , ± 18.75 , ± 16.66 , ± 12.5 , and $\pm 8.3\%$. These 10 shifts were all applied in a pseudorandom order to each regular sequence to create each irregular sequence. Notice that this pseudorandom jittering produced a unique irregular sequence for each regular sequence, regardless of its tempo and pitch. Limiting the maximum deviation to 25% of the IOI prevented the sounds from overlapping or having reversed order.

For the training sessions, four different tempi were chosen: 200, 150, 120, and 100 beats per minute. Their IOIs, respectively, were 300, 400, 500, and 600 ms. The length of each sound was always a quarter of the IOI, so each auditory sound, respectively, lasted 75, 100, 125, and 150 ms. This was applied to maintain the relative timing of each event. For the test sessions, two different tempi were chosen: 171.42 and 109.09 beats per minute. Their IOIs,

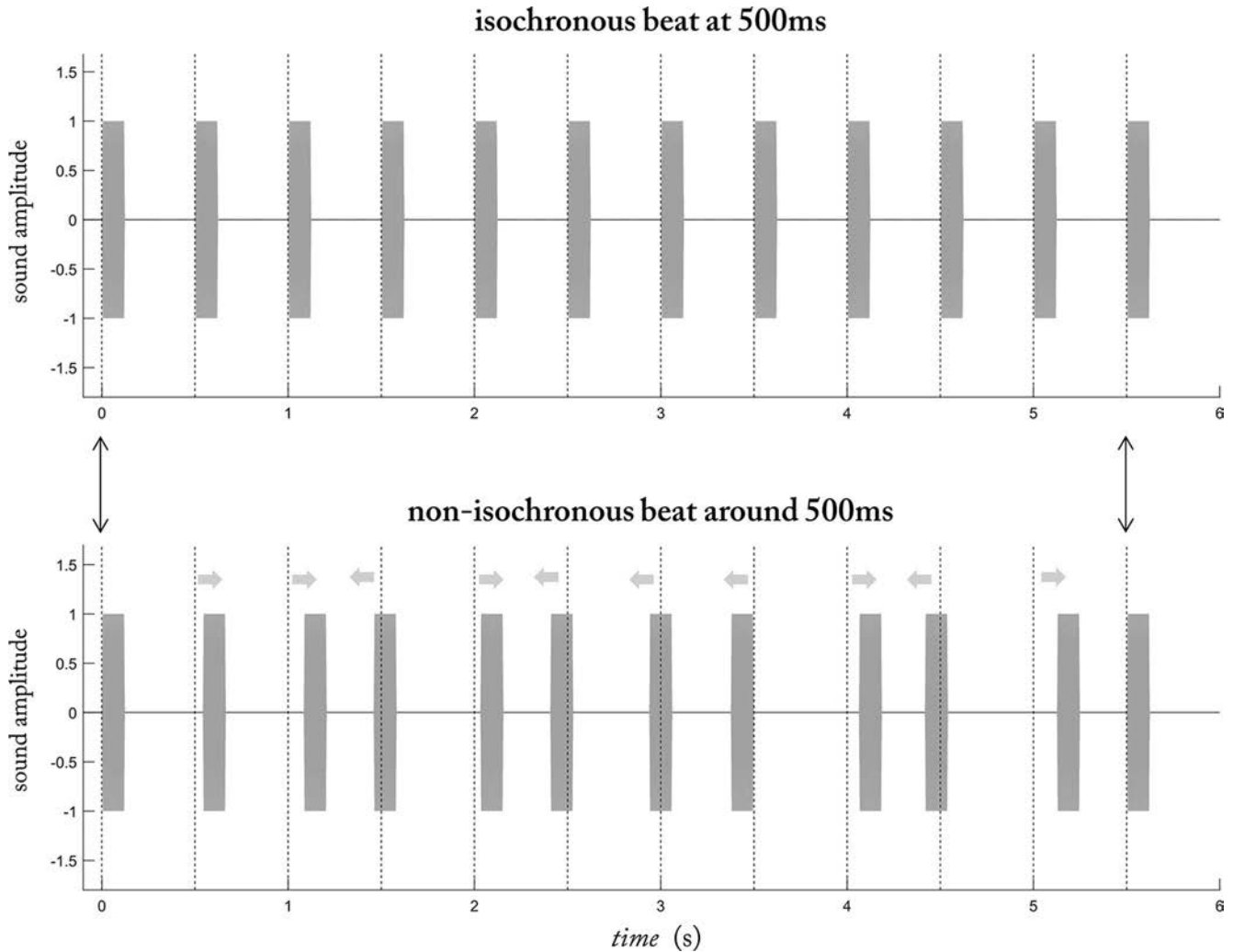


Figure 1. Regular and irregular sound sequences. A sample sequence of 12 regular sounds and its irregular version. Dashed lines mark the onset of sound every 500 ms. Gray arrows indicate the jittering effect on the sound onset in the irregular sequence. Black arrows highlight that both sequences have equal lengths.

respectively, were 350 and 550 ms. Each auditory sound respectively lasted 87.5 and 137.5 ms.

Apparatus. To train and test the rats we used modular response boxes (reference LE1005; Panlab S. L., Barcelona, Spain), equipped with a pellet feeder. Attached to the feeder was a photoelectric detector that registered the nose-poking responses of the rats. Our auditory stimuli were presented using Electro Voice (s-40, Bosch GmbH, Gerlingen, Germany) speakers located next to the boxes. The sound intensity was approximately 68 dB. Each box was isolated within a bigger soundproof box. A custom-made program (RatboxCBC, CBC, Barcelona, Spain) controlled the presentation of stimuli, recorded the nose-poke responses, and provided reinforcement during the study. The nose-poking responses were analyzed using the statistic software SPSS (Version 19, IBM, Armonk, NY).

Procedure. Before the experiment began, rats were trained to put their nose into the feeder to obtain food pellets. They learned the response that triggered food delivery within the first

familiarization session. After the familiarization with the feeder, we started the training. We ran one training session per day. For each session, rats were placed individually in a response box. Forty different stimuli were presented once per session. Twenty of them were regular sequences, and 20 of them were irregular sequences. The intersequence interval was 8 s. During these 8 s of silence, rats automatically received food pellets if a regular sequence was presented, and they positioned their noses into the feeder. Importantly, no food was delivered if the sequence was irregular. The presentation of items was balanced within each session, so there were no more than three items of the same type (regular and irregular) presented consecutively. We also avoided a constant binary alternation of the two types of sequences.

After the training, we tested the discrimination of temporal regularity in rats using novel regular and irregular sequences. To have enough data points, we ran three tests. The first test was run after 30 training sessions, and each of the following tests was run

after 10 additional training sessions. To accommodate all the test items, each test was divided into two sessions. Test sessions included 40 items. From these 40 items, 20 were regular training sequences, 10 were irregular training sequences, and 10 were novel test items (five new regular and five new irregular sequences). The presentation of the test items was randomized within the test session, so that there were never more than two items of the same type in a row. There were 8 s between stimuli. No food was delivered after test items. Thus, during the test, half of the items were reinforced (the 20 regular training sequences) and half were not reinforced (the 10 irregular training sequences plus the 10 novel test items). This was done to avoid the extinction of responses during the test. A three-way repeated measures analysis of variance (ANOVA) was applied to the number of responses rats gave to the novel regular and irregular stimuli during the three tests. The factors were regularity (regular, irregular), tempo (T550, T350), and test (first, second, and third). Post hoc paired *t* tests with the Bonferroni alpha correction were applied to significant main effects and interactions.

All the experimental procedures were conducted in accordance with Catalan, Spanish, and European guidelines and received the necessary approval by the ethical committee from the Universitat Pompeu Fabra and the Generalitat de Catalunya (protocol number 9068).

Results and Discussion

The analyses of the three-way repeated measures ANOVA revealed main effects for regularity, $F(1, 31) = 7.999, p = .008, \eta^2 = 0.205$; tempo, $F(1, 31) = 4.171, p = .0497, \eta^2 = 0.119$; and test, $F(2, 62) = 16.378, p < .001, \eta^2 = 0.346$. There was a

significant interaction between test and tempo, $F(2, 62) = 5.970, p = .004, \eta^2 = 0.161$, but there was no significant interaction between test and regularity, $F(2, 62) = 1.845, p = .167, \eta^2 = 0.056$, tempo and regularity, $F(1, 31) = 0.107, p = .746, \eta^2 = 0.003$, or tempo, regularity, and test, $F(2, 62) = 0.221, p = .802, \eta^2 = 0.007$.

Post hoc pairwise comparisons revealed that rats gave more nose-poking responses for regular ($M = 35.07, SD = 1.44$) than irregular ($M = 33.32, SD = 1.52$) stimuli (mean difference [MD] = 1.76, $p = .008$, 95% confidence interval [CI] [0.49, 3.02]; Figure 2a). Rats responded more during the third test ($M = 39.23, SD = 1.95$) compared to the first test ($M = 29.19, SD = 1.73, MD = 10.04, p < .001, 95\% CI [5.63, 14.45]$) and to the second test ($M = 34.17, SD = 1.59, MD = 5.06, p = .029, 95\% CI [0.41, 9.70]$). They also responded more during the second test compared to the first test ($MD = 4.98, p = .017, 95\% CI [0.73, 9.24]$). The rats gave more responses to the T350 ($M = 34.84, SD = 1.54$) than to the T550 stimuli ($M = 33.55, SD = 1.42, MD = 1.30, p = .0497, 95\% CI [0.00, 2.59]$).

The interaction between test and tempo indicated that rats responded more times for T350 stimuli than for T550 stimuli in the first test ($M_{fast} = 31.94, SD_{fast} = 2.11, M_{slow} = 26.44, SD_{slow} = 1.57, MD = 5.50, p < .001, 95\% CI [-8.21, -2.79]$). Rats did not respond differently for T350 and T550 stimuli in the second test ($M_{fast} = 33.45, SD_{fast} = 1.74, M_{slow} = 34.89, SD_{slow} = 1.74, MD = -1.44, p = .302, 95\% CI [-4.23, 1.36]$) and the third test ($M_{fast} = 39.14, SD_{fast} = 2.11, M_{slow} = 39.31, SD_{slow} = 2.06, MD = -0.17, p = .907, 95\% CI [-3.15, 2.81]$). Figure 3 shows the different responses between the tempi of the stimuli across tests.

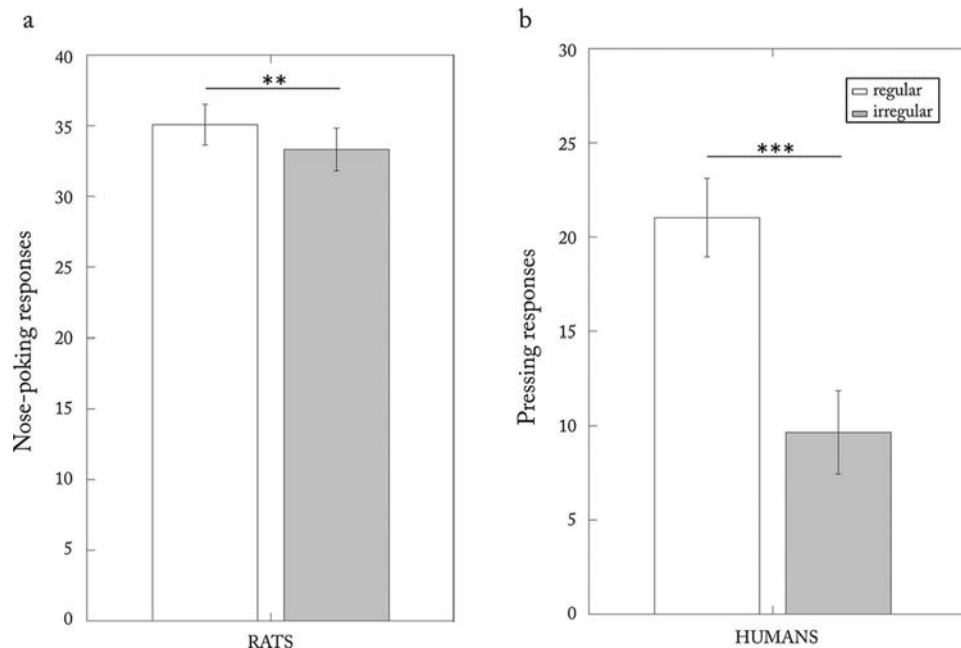


Figure 2. Responses to regular and irregular stimuli. The nose-poking responses of the rats (a) are averaged across the three tests and the two new tempi. The finger-pressing responses of the humans (b) are averaged across the two new tempi. Standard error bars are depicted. ** $p < .01$. *** $p < .001$.

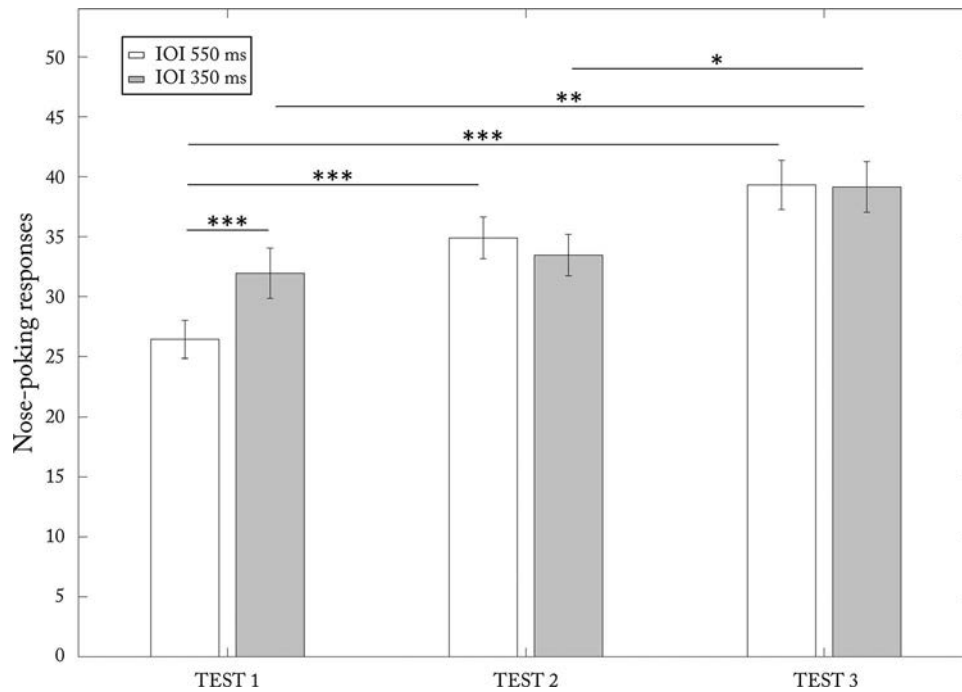


Figure 3. The responses of the rats to T350 and T550 tempi across the three tests. The nose-poking responses are averaged across the regular and irregular stimuli, and their standard error bars are depicted. IOI = inter-onset intervals. * $p < .05$. ** $p < .01$. *** $p < .001$.

The results show that rats gave more nose-poking responses to new regular sequences than to irregular sequences. This suggests that they generalized the discrimination of regularity to novel sequences with different tempi. We also observed that rats produced more responses during the second and third tests, possibly because they got comfortable with the setting used for the go/no-go paradigm. Regarding tempo, the only remarkable finding is that rats responded more times for T350 stimuli than T550 stimuli only in the first test, and not in the subsequent tests. It is an open question whether this finding could be related to a preference for fast auditory rhythms, such as those found in the short ultrasonic vocalizations that rats produce in positive and negative affective states (Saito, Yuki, Seki, Kagawa, & Okanoya, 2016; Sales, 1972). Further research on the rhythmic patterns underlying rats' vocalizations is required to establish any bias toward faster or slower tempi in the processing of rhythms. Similarly, in our experiment, we changed the length of the sounds depending on the IOI. It would thus be interesting to explore whether the animals could be using differences in sound duration as a cue for the discrimination task.

Experiment With Humans

Method

Subjects. Participants were 20 humans (12 female, mean age = 23.49 ± 3.98). No participant had formal training in music or dance, beyond the obligatory education courses. No participant reported any history of hearing, visual, motor, or psychiatric dis-

orders. All participants signed a written consent form and received payment for taking part in the study.

Stimuli. The stimuli consisted of the same auditory sequences used in the experiment with animals. Thus, there were 40 training items: 20 regular sequences and 20 irregular sequences. During the test, we also used the same 10 test items (five regular and five irregular sequences) as with the animals.

Procedure. The study in humans consisted of a single session that lasted approximately 30 min. Participants were seated in a soundproof room in front of a computer. At the bottom of the screen, the image of a small piggy bank and a horizontal empty rectangle was displayed on a black background. Participants listened to the stimuli through headphones (Sennheiser PC 151, Sennheiser Electronic GmbH & Co, Hannover, Germany) at a comfortable hearing level. The visual and auditory stimuli were created using Matlab (v.2013, The MathWorks) and presented with Psychophysics Toolbox extensions (Brainard, 1997). Participants had access to a keyboard, in which a 1 euro cent coin was attached to the spacebar. This attached coin was a cue to start and learn the target behavior of the experiment. We did not give any explicit instructions to the participants in an effort to emulate the training procedure of the rats through the go/no-go paradigm. The only information participants received was that they had to learn alone by pressing the cent on the keyboard. Every time the participants pressed the spacebar, the sound of a dropping coin was heard through the headphones and the image of a big cent of euro appeared on the screen. Immediately after, the number of scored coins appeared above the piggy bank (adding 1 cent of euro per pressing), and the empty bar was filled in with colored area (with

an increase of the size of a pixel from left to right). Participants rapidly learned the relation between pressing the spacebar and scoring one cent of euro. Participants had to press 14 times, to be familiarized with the rewarding procedure, before getting access to the training and test stimuli.

The stimuli were presented in four sections that comprised 40 sequences each. There was also a 6-s pause between each section, in which a sunset landscape appeared on the screen. In these sections, the stimuli were presented in the same order as in the study with the rats. In the first and second sections, all the training stimuli (20 regular and 20 irregular sequences) were presented. In the third and the fourth sections, half of the irregular training stimuli were replaced by the test stimuli (10 regular and 10 irregular sequences). In total, participants listened to 140 training sequences and 20 test sequences. Pressing the spacebar after the regular sequences was reinforced with a cent of euro. The intersequence interval lasted 3 s. This pause gives the participants the opportunity to press up to five times and score 5 cents of euro. Pressing the spacebar after the irregular sequences did not produce any consequence. When the experiment ended, we asked the participants what kind of stimulus gave the reward. All participants received €5 for their collaboration in the study regardless of their scorings.

We ran a two-way repeated measures ANOVA on the number of responses participants gave to the novel regular and irregular test stimuli. The factors were regularity (regular, irregular) and tempo (T550, T350). Post hoc paired *t* tests with the Bonferroni alpha correction were applied to significant main effects and interactions.

Results and Discussion

The two-way repeated measures ANOVA revealed a main effect of regularity, $F(1,19) = 32.033$, $p < .001$, $\eta^2 = 0.628$. There was no main effect of tempo, $F(1,19) = 0.230$, $p = .637$, $\eta^2 = 0.012$, nor an interaction between regularity and tempo, $F(1,19) = 0.828$, $p = .374$, $\eta^2 = 0.042$. Post hoc pairwise comparisons with the Bonferroni alpha correction revealed that humans gave more responses for regular test stimuli ($M = 21.03$, $SD = 2.08$) than for irregular test stimuli ($M = 9.65$, $SD = 2.22$; $MD = 11.38$, $p < .001$, 95% CI [7.17, 15.58]; Figure 2b). There were no differences between T350 ($M = 15.18$, $SD = 1.93$) and T550 ($M = 15.50$, $SD = 1.93$) responses ($MD = 0.33$, $p = .637$, 95% CI [-1.09, 1.74]). Our results thus corroborate that humans distinguish regular from irregular sequences using exactly the same stimuli that we used to test the rats.

Eleven out of 20 participants clearly responded that regular sequences were the key to score the coins. To refer to isochrony, these participants used terms as “regular,” “constant sounds,” or “same/continuous rhythms.” The participants who did not give an appropriate answer reported other hypotheses. Five of them considered that an accurate repetition of the rhythm was the key to receive reward and found the regular sounds easy to follow. Four of them speculated that the tempo and/or pitch of the sounds could be important cues to press and score the coins. A similar discrimination could be assumed for musicians, who are extensively trained to perceive and produce rhythms. Supporting evidence comes from the work by Madison and Merker (2004), who found that musicians and nonmusicians similarly applied phase correc-

tion and period correction strategies to compensate deviations of 3 to 96 ms from isochrony in a finger-tapping task. Besides, musicians and nonmusicians responded alike when they had to judge the presence of regularity and irregularity in quasi-isochronous sequences of sounds (Madison & Merker, 2002). These studies suggest that our stimuli would be clearly perceived as regular or irregular for both musicians and nonmusicians.

General Discussion

The present study explores the first cognitive step for beat perception, the detection of regularity, in two mammal species. We presented rats and humans with regular and irregular sequences of sounds. We observed a greater number of responses to novel regular sequences than to novel irregular sequences in both species. This was more evident for humans than for rats, despite the greater number of training sessions that rats received. We also found that rats changed their nose-poking responses at the first test based on the tempo of the stimuli. No effect of tempo was found for humans. Our findings suggest that rats can learn to discriminate regular from irregular sequences of sounds and generalize this discrimination to sequences with novel tempi.

In this study, the subjects were trained with sound sequences implemented at five different pitches and four distinct tempi that maintained the relative durations of the sounds depending on each IOI. The use of several acoustically different training items may have helped the individuals to pay attention to global features to discover the rewarding sequences. In fact, both species generalized their responses to the test sequences, where the sounds had new absolute durations. This indicates that the individuals used relative durations to identify the regular items. That is, our results suggest that rats may have identified “isochrony” regardless of the absolute durations (for contrasting results with zebra finches, van der Aa et al., 2015). Due to our paradigm, we cannot disentangle whether the detection of isochrony is achieved by interval-based timing mechanisms alone or in conjunction with beat-based timing mechanisms. This means that our findings are neutral to the gradual audiomotor evolution hypothesis, which proposes that beat-based timing gradually appeared in the primate lineage (Honing, Bower, Prado, & Merchant, 2018). We cannot know whether rats were focusing on the whole sequence or just the last intervals to detect regularity, which could inform about the use of an interval-based memory or adjacent mechanism (Keele et al., 1989). This could be tested in the future with shortened sound sequences.

Previous studies have indirectly tested the processing of regularity in other rodents and macaques. For instance, Herry et al. (2007) found that the unpredictability of the irregular stimuli elicited more activity in the amygdala and anxiety-like behavior in mice. Unfortunately, we do not know whether rats experimented similar anxiety-like behaviors that could have interacted with a preference of regularity over irregularity. What is clear is that rats behaviorally discriminated temporal regularity in the sequences of sounds, which could be linked to their neural sensitivity to omitted isochronous sounds (Jongsma et al., 2002). In rodents, this sensitivity could go beyond isochrony, as in the anesthetized gerbils who show electrophysiological differences for sounds in on-beat and off-beat positions (Rajendran et al., 2017). In contrast, Honing and colleagues (2018) did not find differences in the mismatch negativities of two macaques that processed deviant tones in

on-beat and off-beat positions. The differences appeared regarding the regularity of the stimuli: larger mismatch negativities for regular sequences compared with the jittered ones (Honing et al., 2018). As in our behavioral study, macaques seem to be sensitive to the perception of regularity. This sensitivity to regularity in macaques is also supported by the electrophysiological responses to deviating sounds in the sequential grouping of triplets (Selezneva et al., 2013). More research using electrophysiology may elucidate where acoustic regularity detection and beat perception appears across species with similar neural structures underpinning the integration of temporal events.

The findings presented here suggest that the perceptual timing mechanisms underlying regularity detection are not limited to vocal learners. As Herry and collaborators (2007) postulated, many organisms might share a template of regular patterns to reduce the complexity of sensory information and thus evaluate the environment for potential dangers. If so, many species should be able to detect perceptual regularities in the environment regardless of their modality. This seems to be true for nonhuman primates and monkeys, who are sensitive to auditory and visual regular stimuli (Merchant & Honing, 2014; Takeya, Kameda, Patel, & Tanaka, 2017). In addition, an interesting open question is whether irregular stimuli might be aversive to individuals across species. In the present experiment, we reinforced the regular sequences, but it would be interesting to explore whether similar results could be observed if we would reinforce the irregular sequences instead of the regular ones. That is, it might be the case that animals exhibit a preference toward regular stimuli and might find irregular stimuli aversive as has been suggested by the work of Herry and collaborators (2007). The results we observed here suggest that rodents readily discriminate between regular and irregular sequences. Together with previous animal studies (Ravignani & Madison, 2017), it seems that detecting regularity across modalities could be fundamental to organize perceptual events over time. The combination of behavioral and electrophysiological research will elucidate up to what point the cognitive processes underlying musical rhythms are shared across species.

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