



Production of regular rhythm induced by external stimuli in rats

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Abstract

Rhythmic ability is important for locomotion, communication, and coordination between group members during the daily life of animals. We aimed to examine the rhythm perception and production abilities in rats within the range of a subsecond to a few seconds. We trained rats to respond to audio-visual stimuli presented in regular, isochronous rhythms at six time-intervals (0.5–2 s). Five out of six rats successfully learned to respond to the sequential stimuli. All subjects showed periodic actions. The actions to regular stimuli were faster than randomly presented stimuli in the medium-tempo conditions. In slower and faster tempo conditions, the actions of some subjects were not periodic or phase-matched to the stimuli. The asynchrony regarding the stimulus onset became larger or smaller when the last stimulus of the sequence was presented at deviated timings. Thus, the actions of the rats were tempo matched to the regular rhythm, but not completely anticipative. We also compared the extent of phase-matching and variability of rhythm production among the interval conditions. In interval conditions longer than 1.5 s, variability tended to be larger. In conclusion, rats showed a tempo matching ability to regular rhythms to a certain degree, but maintenance of a constant tempo to slower rhythm conditions was difficult. Our findings suggest that non-vocal learning mammals have the potential to produce flexible rhythms in subsecond timing.

Keywords Rhythm · Synchronization · Entrainment · Subsecond timing · Rat

Introduction

The ability to synchronize actions with external events is widely exhibited in our daily lives, such as in music, conversation, and coordinated behavior. Following Patel et al. (2009), synchronization requires that sequential actions, such as finger tapping or head bobbing, match both the tempo and phase of external rhythmic stimuli, that is, the production of actions at regular intervals in accordance with the stimulus, and close to its onset (Patel and Iversen 2014). Precise synchronization to the complex rhythmic sequences (i.e., beat) of a wide range of tempi has been found in limited species to date, such as human and parrots (Hasegawa et al. 2011; Patel 2014), which are both vocal learning species. Therefore, the vocal learning and rhythmic synchronization hypothesis has been proposed (Schachner et al. 2009). This hypothesis states that the ability of advanced motor

synchronization evolved as a by-product of selection for vocal mimicry (Patel 2006).

Under experimental settings, spontaneous and trained motor synchronization have been examined for non-vocal learners. Spontaneous synchronization to external auditory stimuli has been reported in chimpanzees (*Pan troglodytes*, Hattori et al. 2013) and bonobos (*P. paniscus*, Large and Gray 2015). After intensive training (for over a year), rhesus monkeys (*Macaca mulatta*) learned to produce a regular rhythm by tapping to an auditory or visual metronome (Zarco et al. 2009). These studies suggest that non-human primates that are non-vocal learners, exhibit motor synchronization to isochronous rhythms, though within a limited tempo range. Merchant and Honing (2014) proposed that synchronization to complex rhythms (i.e., beats) in humans has gradually developed in the primate lineage. However, it is known whether motor synchronization is learnable for only primates or the ability is shared with a wide range of non-vocal learning mammals. An example of an operant conditioning study of the California sea lion (*Zalophus californianus*, Cook et al. 2013) revealed that they exhibit flexible synchronization to music. However, whether they are indeed non-vocal learners was not formally confirmed;

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pinnipeds are reported to have some degree of volitional vocal control (Reichmuth and Casey 2014). Rhythmic movements involving interactions with external events are broadly displayed by various species during locomotion, communication, and coordination between group members, possibly because it is advantageous (Larsson 2012, 2014; Wang 2015). It is hypothesized that coordinated group movements have evolved because they reduce incidental sounds of locomotion, and improve hearing perception (Larsson 2012; Larsson and Abbot 2018). Therefore, it is expected that motor synchronization to regular rhythms within a limited tempo range is also present in non-primate species. The examination of regular rhythm production in non-vocal learning species other than primates contributes to our understanding of how ecological or social factors, in addition to phylogenetic factors, have affected the evolution of the motor synchronization ability.

Rats (*Rattus norvegicus*) are model species for various research topics, including timing perception and production. Previous studies have revealed that rats can detect the regularity in 200-ms interval tone sequences (Noda et al. 2017) and learn to produce lever pressing action in 700-ms (non-sequential) intervals without external cues (Kawai et al. 2015). Moreover, a study on collaborative behavior reported synchronization with conspecifics; rats successfully learned to quickly press a lever in response to a partner's response within 500 ms of asynchrony with the partner (Tan and Hackenberg 2016). These studies found that rats exhibited sensitivity to rhythmical sequences, and were able to produce action for a single interval in a subsecond range. However, it is unknown whether rats can follow and respond to sequential, regular stimuli and, moreover, predict the timing of the regular stimuli.

We aimed to clarify the rhythm perception and production abilities in rats within the range of a subsecond to a few seconds. We examined whether rats could acquire lever pressing in time to a regularly presented stimulus. We used both auditory and visual stimuli, because a unimodal task such as an auditory (Hasegawa et al. 2011) or visual task (Zarco et al. 2009) conducted in previous studies seemed difficult for rats. First, we examined whether rats produced periodic actions in each tempo. We then investigated whether rats anticipated the regularity of the stimulus via two tests. We predicted that they would respond more quickly to the regular, predictable stimuli than to the randomly presented, unpredictable stimuli sequence, following the methodology described by Hasegawa et al. (2011). We also predicted that when the presentation of the last stimulus of the sequence was delayed compared to the previous stimulus, the asynchrony between the action and onset of the last stimulus would be shorter than that of the previous stimulus, and vice versa. This was assumed because if the rats maintained the tempo of the sequence, and did not merely respond to each

stimulus, the action would deviate from the actual timing of the irregularly presented stimulus. The interval for each stimulus ranged from 0.5 to 2 s. We compared the asynchrony with the stimulus onset and variability of interval production according to the target interval length. We predicted that the subjects would perform better for the shorter interval conditions especially those less than 1 s, as has been observed in humans and macaques (Zarco et al. 2009).

Materials and Methods

Ethics statement

The experiments in the present study were conducted in accordance with the experimental implementation regulations of the University of Tokyo. This study was approved by the animal experimental committee at the University of Tokyo, Graduate School of Arts and Sciences (Permission Number: 27-8).

Subjects and housing

Six male Long-Evans rats (Japan SLC, Inc., Shizuoka, Japan) 10 weeks old at the beginning of the experiment were the subjects of the study. One subject was unable to achieve the training criteria; therefore, only the data of five subjects were used in the analyses. The subjects were housed in pairs under a temperature of 23 ± 2 °C and a 12-h light/dark cycle (lights on at 8:00 am). Prior to the start of the experiment, the rats were provided free access to food for two weeks, and then restricted to 16 g per day during the experiment. Water was available ad libitum in their home cage.

Apparatus

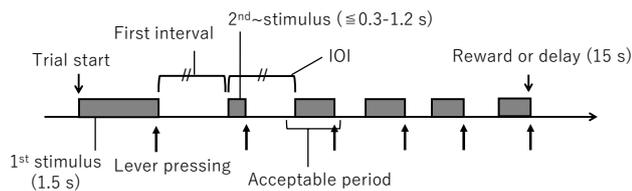
We used a Skinner box (interior 330 W × 300D × 250H mm, OPR-3601, O'Hara & Co., Ltd, Tokyo, Japan) that was equipped with two levers, feeders, and LED lights bisymmetrically placed in a soundproof box (MC-050/CMTUII, Muromachi Kikai, Tokyo, Japan). Two loud-speakers (AT-SP93, Audio-Technica, Tokyo, Japan) were situated on the outside of the Skinner box, one on either side of the levers. The box was partitioned into two compartments by a wire mesh wall in the center. Each subject was trained in one of the compartments (left or right) throughout the experiment. The lever pressing behavior of the rats was recorded by a computer with accuracy in milliseconds.

Stimuli

One trial consisted of five or six stimuli presentations, which were presented in a regular metronomic tempo

Table 1 Inter-onset interval, stimulus duration, and acceptable period for each trial condition

Study period	IOI (s)	Stimulus duration (s)	Acceptable period (s)
1	2	1.2	1.4
1	1.5	1	1.2
2	1.2	0.8	1
2	0.9	0.6	0.8
3	0.7	0.45	0.57
3	0.5	0.3	0.42

**Fig. 1** An example of a regular trial consisting of six stimuli. Inter-onset intervals (IOIs) were fixed during each trial except for the first stimulus. The duration of intervals from the offset of the first stimulus to the onset of the second stimulus was the same as the IOIs of the second stimulus and all stimuli thereafter. The stimulus was immediately turned off when the lever was pressed

(regular trial). A yellow LED light and 10 kHz pure tone with a sound pressure level of 60 dB were used as the stimuli. Six inter-onset interval (IOI) conditions were used: 2, 1.5, 1.2, 0.9, 0.7, and 0.5 s, for which the corresponding stimulus durations were 1.2, 1, 0.8, 0.6, 0.45, and 0.3 s, respectively (Table 1). The IOIs of the stimuli were fixed during each regular trial, except for between the first two stimuli. The duration of the first stimulus was 1.5 s for all conditions. The interval between the first response and the onset of the second stimulus was the same as the IOI of each condition (Fig. 1). For example, in a trial with a 2 s IOI, the second stimulus was presented 2 s after the response to the first stimulus, and the third stimulus was presented 2 s after the onset of the second stimulus. This was done with the intention of lowering the difficulty of the task. An acceptable period was set before and after a stimulus, and the lever pressing that occurred during this acceptable period was counted as a correct response. The margin of the acceptable period before and after a stimulus was 0.06 s for 0.3 or 0.45 s stimuli, and 0.1 s for 0.6 to 1.2 s stimuli (Table 1). Correct response to a trial was reinforced with a 20 mg purified rodent tablet (5TUL, TestDiet, St. Louis, US) and an 8.6 kHz reward sound was played for 1 s.

Study periods and sessions

The experiment was composed of three periods based on the tempo of the stimulus sequences. IOIs were 2 and 1.5 s in the first period, 1.2 and 0.9 s in the second period, and 0.7 and 0.5 s in the third period. To lower the difficulty of the task, only two interval conditions were used in each period. The order of the study period was the same for all subjects because it was difficult for them to lengthen intervals of lever pressing behavior. One session continued until trial counts reached 200 or for 60 min, with the exception of habituation (on the first day). The two tempi of the trials were presented in a quasi-random order in each session.

Training

One training or test session was conducted daily. On the first day of the first study period, rats were habituated in the box and the feeder (30 min). Then, the lever pressing behavior was shaped for one or two sessions. To shape the rats to press the lever in time to the regularly presented stimulus, stepwise training was conducted from one to five or six consecutive pressings of the lever to a regular stimulus (two subjects completed the training of six consecutive pressings, but three subjects did not, see below). Initially, lever pressing during a stimulus presentation (5 s) was reinforced. Stimuli were turned off immediately after the correct response was achieved. When a rat achieved a correct response rate of 75% in two consecutive sessions, training was moved on to the next stage. In this training, the first two stimuli of a regular trial were presented. When a rat responded correctly to these two stimuli, the trial was counted as successful. After this stage of the training, lever pressing outside of the acceptable periods during a trial was counted as an error response, and the trial was immediately terminated and a 15 s delay period was inserted. The number of stimuli presented was increased in the same way. When the rats achieved a correct response rate of 75% in the training of five or six consecutive pressings in two successive sessions, test phases were conducted. Three subjects (K4, K6, and K7) took over 30 sessions to achieve five consecutive pressings, so were subsequently moved on to the test phase, skipping the six consecutive pressings training.

After the completion of the test phases during the first period, the training of the second study period commenced. Similarly, after the completion of the second period, the third study period commenced. The second and third study periods started with the five or six pressings training. If the correct response rate remained lower than 20% for two sessions, we retrained the rats in the prior training stage (four or five lever pressings) for the new interval conditions. One subject (K7) could not achieve 1.5 s- and 2 s-interval

conditions after 60 training sessions, so was excluded from the analyses for these conditions.

Test trials

Two test phases were conducted in each study period, after the rats had completed the training of that period. The test phases were continued for five sessions each to obtain a sufficient number of trials for the data analysis. Between the test phases, two or three training sessions were conducted. To avoid the test trials being learnt, 10% of the trials (20 trials) were replaced by test trials during each test session. Test trials were presented in a random order in each session.

To obtain the true reactive response time, we presented all stimuli at random intervals (random trial) in the first test phase. In this random trial, the intervals were randomly generated by a 0.05 s order within the range of the intervals being used during that training phase. The average interval in the random trial was set to the average value of the two training intervals. The stimulus duration was the average of two training trials, and the margin of the acceptable period was the same as that for the training trials.

The second test phase was conducted to examine whether the rats showed anticipative rather than reactive lever pressing. In these test trials, stimuli except for the last stimulus were presented in either of the tempi used during that training phase, and then the last stimulus was presented in another tempo (irregular trial). For example, during an irregular trial of the first period, stimuli were presented at 1.5 s intervals until the fourth or fifth stimulus, then the last stimulus was presented after a 2 s interval. The duration and margin of the acceptable period of the last stimulus were the same as those of the former stimuli in that trial.

Data analyses

We conducted all analyses in R version 4.0.2 (R Core Team 2020) and the package ‘circular’ (Agostinelli and Lund 2017) for Rayleigh test and Mardia-Watson-Wheeler test, and ‘lme4’ (Bates et al. 2015) for ANOVA. All tests were two-tailed with a significance level of $p < 0.05$. For the analyses of periodicity and comparison among the interval conditions, we used the data from the last five training sessions prior the first test session in each period. We carried out analyses on an individual basis, except for the comparisons among intervals. When the same analyses were conducted multiple times within individuals, results were adjusted using the Bonferroni method.

Inter-response interval

The inter-response interval was defined as the interval between the onset of two subsequent lever pressings. We examined

whether the actions of the rats matched the tempo used. We used Rayleigh test of uniformity, which examines whether circular data is distributed in a unimodal manner, thus analyzing the periodicity of the data. For this analysis, we pooled the trials of five training sessions according to each interval condition. The next two analyses were only conducted for conditions in which significant periodicity was confirmed.

Asynchrony with the stimulus onset

We calculated the asynchrony between the lever pressing and stimulus onset in milliseconds. If a rat responded during the acceptable period but before the stimulus presentation, the asynchrony took a negative value. We compared the asynchrony to the last stimulus of the random and regular trials via the Mardia–Watson–Wheeler test, which examines homogeneity between two samples of circular data. We examined whether rats anticipated the regularity of the stimulus.

To examine whether the rats maintained the tempo of the stimulus sequence, we compared the asynchrony with the last stimulus and that with the prior stimulus in irregular and regular trials. Two-way repeated measures ANOVAs were conducted on the average values of asynchrony in each five test sessions for each condition. The explanatory variables were the trial condition (irregular/regular), stimuli order (the last/the prior), and their interaction. When the interaction was significant, the effect of the stimuli order was examined separately according to the trial conditions using *t*-test.

Comparison among intervals

We examined the extent of phase-matching and variability by the target intervals. We predicted that the action of rats would be more phase-matched and less variable in shorter intervals. We compared the asynchrony and variability of asynchronies by one-way repeated measures ANOVA. The variability of asynchronies was calculated by the dividing the standard deviation of the asynchronies by the target interval length. As two interval conditions (1.5 and 2 s) were missing for one of the subjects, ANOVAs were conducted using linear mixed models for these analyses. The fixed and random effects were the interval condition, and subject id, respectively. When the effect of the interval conditions was significant, a pairwise comparison using *t*-test with the Holm method was conducted.

Results

Comparison within individuals

Five rats achieved the training criteria in 154.3 ± 15.6 training sessions during the first period, 56.2 ± 25.1 sessions during the second period, and 27.6 ± 12.2 sessions during the third period. Rayleigh test revealed that all rats showed consistent periodicity in the 0.9-s and 1.2-s interval conditions, and four out of five rats showed consistent periodicity in 0.5-s and 0.7-s interval conditions ($p < 0.05$, Table S1). Out of four rats that carried out 1.5-s and 2-s interval conditions, two and three rats, respectively, showed periodic actions (Table S1).

Figure 2 shows the modes of distribution of lever pressing actions in each subject. The asynchronies in the regular trials were significantly different from those in the random test trials, except for one subject in the 1.5-s interval condition (Watson–Wheeler test with Bonferroni correction, $p < 0.05$, Table S2). The modes in regular trials were significantly shorter than those in random trials, except for one subject in the 0.5-s and 0.7-s interval condition (Fig. 2). This indicates that rats produced action faster than when they produced

action in a completely reactive manner in most interval conditions.

The asynchrony with the onset of the last stimulus in the irregular trials is summarized in Table 2. We compared the asynchrony between the last two stimuli in the regular and irregular trials. If the rats made the actions at the same tempo as that of the previous stimulus, the asynchrony was predicted to be shorter than before in the condition where the last stimulus was presented later (IOI: 1.5, 0.9, and 0.5 s) and to be longer in the condition where the last stimulus was presented earlier (IOI: 2, 1.2, and 0.7 s) than the regular tempo used in the test. A significant interaction between the stimulus order (the last vs. the prior) and trial condition (regular vs. irregular) was found in 13 of the 23 analyzed conditions (two-way repeated measures ANOVA; $p < 0.05$). Post-hoc analyses revealed that the asynchrony between the last and the prior stimuli in the irregular trials was significantly different (t -test with Bonferroni correction, cells in bold in Table 2), whereas there was no significant difference regarding this aspect in the regular trials (Table S3). Therefore, the asynchrony changed when the last stimulus was presented at an irregular tempo. However, as predicted, three of the four subjects showed a shorter asynchrony for the 0.5-s interval under the irregular conditions (Table 2;

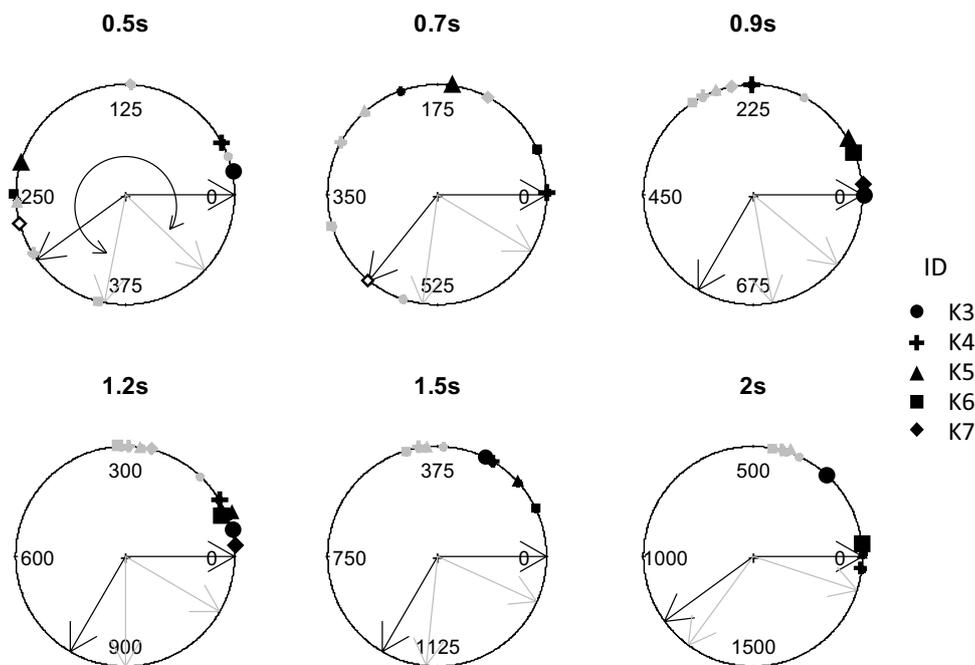


Fig. 2 Circular plots of the regular and random trials in each interval condition. Black markers indicate the modes of distribution of the regular trials in each subject, while gray markers indicate those of random trials. Large black markers indicate the data points that were significantly shorter than those in the random trials, open markers indicate the data points that were significantly longer than the random trials, and small black markers indicate that was not significant in this

or prior analyses. Two overlapped data points in the 1.2 s interval condition were described with jitter. Black arrows indicate the onset (0 degree) and offset of the stimulus presentation, while gray arrows indicate the onset and offset of the acceptable period. An example of an acceptable period (0.5 s) is described by an arc inside the circle. Axis labels inside the circle indicate time (ms)

Table 2 Average asynchrony to the last stimulus in the irregular trials

Period	Interval	Asynchrony (ms) and F value of the interaction between the condition and stimuli order (df = 1, 8)					
	ID	K3	K4	K5	K6	K7	
1	2s	488.4 (0.020)	494.3 (0.243)	-	442.5 (5.338)		slow
	1.5s	320.9 (0.227)	-	354.2 (0.149)	-		fast
2	1.2s	154.6 (1.589)	303.5 (0.185)	84.2 (6.407)	122.2	260.3 (5.020)	
					(11.900)		
3	0.9s	269.0 (6.851)	383.1 (7.206)	274.9 (0.144)	230.1 (9.676)	296.2 (5.061)	
	0.7s	396.8 (7.207)	-	447.5 (6.693)	268.7 (0.523)	101.0 (0.486)	
	0.5s	184.7	-	331.2 (0.617)	155.4	91.0	
		(17.869)			(16.460)	(-10.108)	

The conditions that were significantly different from the prior stimulus by ANOVA and post-hoc test are highlighted in bold. The values in parentheses are F values of the interaction between the trial condition (regular vs. irregular) and stimuli order (prior vs. last). Underlined values indicate that the asynchrony was significantly longer than that in the regular trials, while plain values indicate that the asynchrony was significantly shorter than that in the regular trials. The row colors indicate the two types of irregular trials: gray rows indicate the conditions in which the last stimulus was presented earlier than the regular tempo, and plain rows indicate the conditions in which the last stimulus was presented later than the regular tempo. The results were adjusted using Bonferroni correction. The conditions that are blank were not significant according to Rayleigh test

Fig. 3a [K6]), while the asynchrony in four of the five rats became longer in the 0.9-s interval under the irregular condition (Table 2; Fig. 3b [K4]). In these two irregular trials, the last stimulus was delayed compared to that in the corresponding regular trials. Thus, the subjects did not always press a lever to the last stimulus, instead maintaining the tempo of the previous stimuli.

Comparison among interval conditions

The average mode of action for all subjects according to the interval conditions in the regular trials is shown in Fig. 4a. One-way repeated measures ANOVAs revealed that the effect of the interval on asynchrony was significant ($N=5$, $F [1, 4]=3.746$, $p=0.016$). However, there were no significant differences between the interval conditions (pairwise comparison using t-test with the Holm method, $p > 0.1$). Therefore, the prediction that the actions were more phase-matched in the shorter interval conditions was not supported.

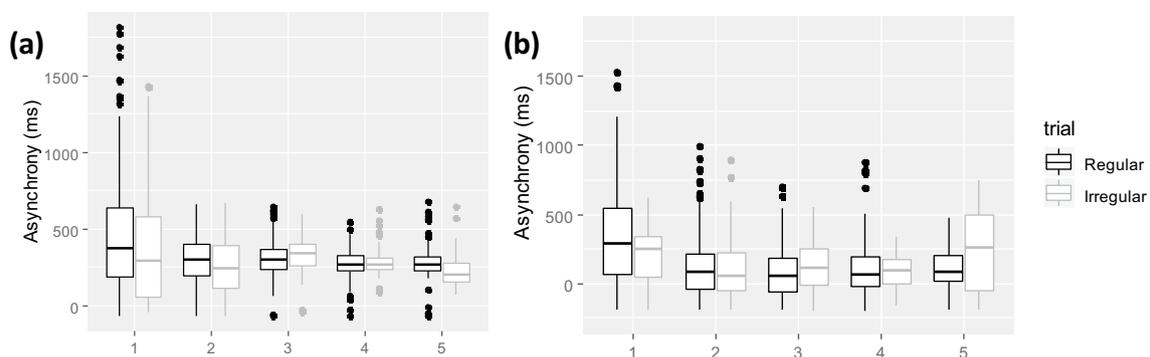


Fig. 3 Examples of changes in the asynchrony with the stimulus onset during a trial. The horizontal axis indicates the order of the stimuli presented. **(a)** Asynchrony of K6 in the regular (black) and

irregular (gray) trials during period 3 (IOI: 0.5 s). **(b)** Asynchrony of K4 in the regular (black) and irregular (gray) trials during period 2 (IOI: 0.9 s)

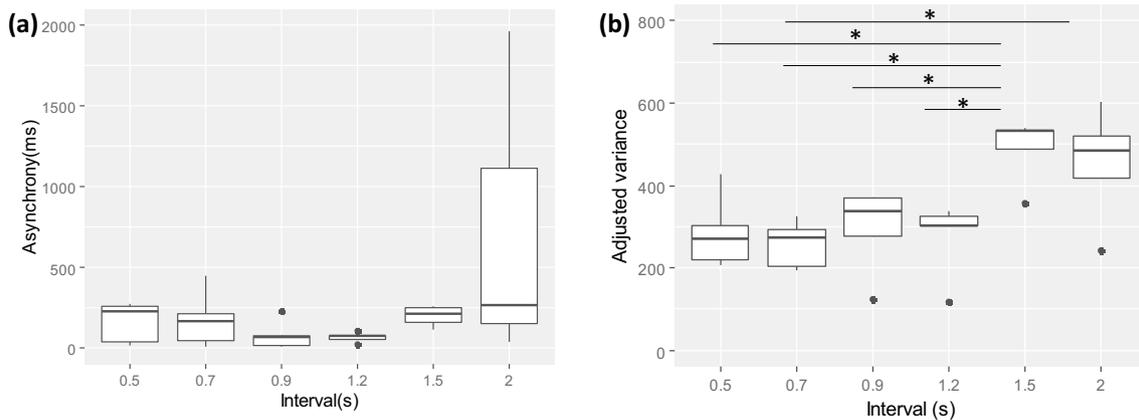


Fig. 4 Boxplots of (a) the asynchrony with the stimulus onset and (b) adjusted variance of the last stimulus in the regular trials for each trial condition ($N=5$). The adjusted variance was calculated by dividing

the standard deviation by the target interval length. Asterisks (*) indicate significant differences $p < 0.05$ according to one-way repeated measures ANOVA and pairwise t test, Holm method

The average adjusted variability of asynchrony within each individual was significantly different between intervals (one-way repeated measures ANOVA, $N=5$, $F [1, 4] = 8.523$, $p = 0.0003$; Fig. 4b). The adjusted variability of the 1.5-s interval condition was larger than that of the 0.5–1.2 s interval conditions, and that of the 2-s interval condition was larger than the 0.7-s interval condition (pairwise comparison using t -test with the Holm method). Rats showed higher variability in their actions, particularly for the longer interval conditions.

Discussion

To the best of our knowledge, this is the first study to investigate the rhythm production ability of rats. Rats learned to respond to regularly presented audio-visual stimuli after 4–5 months of training. Previous studies have revealed that budgerigars did not require special training (Hasegawa et al. 2011), while monkeys needed over a year of training to learn an auditory-motor synchronization task (Zarco et al. 2009). Compared to the other above-mentioned studies, the task in our study included fewer interval conditions in one period, and contained both auditory and visual stimuli. Even when considering the various differences, the synchronization task was as difficult for our rats as it was for the monkeys.

All subjects exhibited periodic actions in the 0.9-s and 1.2-s interval conditions, but one or two subjects did not show clear periodicity in the other intervals. We assumed that the asynchrony in the random trials was a reactive response. Based on this, rats were considered able to predict the regularity of the stimuli and produce tempo-matched actions at least in the 0.9-s and 1.2-s tempo range. In the 0.5-s and 0.7-s interval conditions, the asynchrony of one

subject was longer than that in the random trials. The subjects were not trained to match their action to the stimulus onset; they could get the reward only if they responded during the acceptable period. This may be the reason that one rat showed periodic actions that were out of phase and instead made actions near the offset of the stimulus. Human and parrot species tend to show actions preceding the actual stimulus by a few tens of milliseconds (Hasegawa et al. 2011; Patel 2014) in what known as negative mean asynchrony (Repp 2005). Our subjects did not show negative mean asynchrony. These findings indicate that rats do not tend to phase-match to the stimulus, and their actions are not completely anticipative in contrast to parrots and humans.

Irregular trials were performed with the intention of investigating whether rats maintained the tempo induced by the stimuli that had been presented previously. If the tempo was maintained, it was predicted that the asynchrony would become shorter when the last stimulus was presented later than the previous interval used in the trial, and vice versa. The subjects performed the action at a deviated time in the irregular trials; however, they did not maintain the previous tempo in all conditions, unlike what we had predicted. This is probably because rats made some prediction of stimulus timing and prepared for the action, but the action was still dependent upon the actual stimulus presentation. Therefore, this indicated that the rats did not strongly rely upon the internal rhythm induced by the stimuli.

We predicted that rats would show more accurate actions in shorter interval conditions; however, this was not completely supported by our results. There were no differences in the asynchronies among the interval conditions. There was a larger variability in the 1.5 s interval condition than in those below 1.2 s, though the differences between the 2-s and 1.2, 0.9, and 0.5-s interval conditions were not significant, probably because of the

large variability among the subjects. Previous studies in humans, macaques (IOI: 0.45–1 s, Zarco et al. 2009), and budgerigars (IOI: 0.45–1.8 s, Hasegawa et al. 2011) have highlighted an increase in the variability of tap intervals as the target interval increase. In comparison, our findings did not show less variability especially in shorter intervals; rather, they showed a good performance in the 0.9-s or 1.2-s interval conditions in two tests. Previous studies have shown that in rats the production of action to the precise interval of 0.7 s required intensive training (35 days, Kawai et al. 2015), whereas they detected regular rhythm (IOI: 0.6 s) spontaneously (Noda et al. 2017). Thus, rats have a sensitivity to a quick tempo, but the precise motor control at such a tempo is relatively weak. At the least, we can conclude that rats have difficulty in keeping up with constant tempo in intervals longer than 1.5 s. As stated in Larsson (2012), if coordinated locomotion is the preadaptation of rhythm perception and production, our result is consistent with the statement as a slow tempo (IOI > 1.5 s) is far from the natural locomotion of rats. Some researchers have highlighted that it is important to consider an animals' natural propensity when selecting stimuli and behavioral responses in synchronization experiments (Wilson and Cook 2016; Hoeschele et al. 2015). We might be able to improve the performance of rats in quick tempi by examining locomotive action, which may be more natural and has less load for rats. In addition, it would be fruitful to investigate the effects of the locomotive style of the species and the environments the species usually live in on the synchronization ability to external stimuli.

In conclusion, rats have some tempo matching abilities to regular rhythms, but do not possess a phase matching ability. In a review of the regularity perception in birds, it was concluded that there is no strong divide between vocal learners and non-vocal learners concerning sensitivity to regularity (ten Cate and Spierings 2018). In addition, the study on sea lion indicates that skill of extracting a beat from a stimulus sequence is trainable (Wilson and Cook 2016). Our study revealed that not only primates, but also other non-vocal learning mammals have the potential for flexible rhythm production. This finding indicates the possibility that a common evolutionally background and neural basis for rhythm production exist in mammals, and future studies will be able to examine it by developing physiological studies in rats. Rats are highly social (Lopuch and Popik 2011; Rutte and Taborsky 2007; Tan and Hackenberg 2016) and communicative (Brudzynski 2013; Seffer et al. 2014) species. Several studies have proven that the social situation facilitates entrainment (Connor et al. 2006; Kirschner and Tomasello 2009). Further experiments on whether the synchronization ability would be better demonstrated under social situations may

contribute to a better understanding of the evolution of beat perception and entrainment.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10071-021-01505-4>.

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Data availability Data are provided as electronic supplementary materials.

Compliance with ethical standards

Conflict of interest Authors declare that they have no conflict of interest.

Ethical approval The experiments in the present study were conducted in accordance with experimental implementation regulations of the University of Tokyo. The present study was approved by the animal experimental committee at the University of Tokyo, Graduate School of Arts and Sciences (Permission Number: 27-8).

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