

Effect of temporal separation on tone-sequence discrimination in monkeys

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Abstract

Perception of auditory spectral–temporal patterns was examined in two Japanese monkeys. The stimuli used were pairs of pure tones of different frequencies that were presented sequentially. The monkeys were required to discriminate whether the frequency of the second tone was higher or lower than the first tone. The performances of the monkeys deteriorated when a temporal gap (i.e., silence) was inserted between the component tones. A comparison experiment did not show such effects in human participants. The results suggested that monkeys use frequency transitions for tone-sequence discrimination, and that local characters are more dominant discrimination cues in monkeys than in humans.

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Key words: Auditory discrimination; Tone sequence; Japanese monkey

1. Introduction

Perception of relative properties in auditory sequences is essential in perceiving human speech. Human speech consists of sequences of sounds, and listeners have to perceive the spectral–temporal relation of the component sounds. A comparison of the properties of such auditory organization between humans and other species may help us understand the evolution of the human auditory system. Similar to humans, Japanese monkeys possess a wide variety of vocalizations related to their social behavior (Itani, 1963; Green, 1975). Their vocalizations usually involve frequency and amplitude modulation, but vocal sequences with multiple syllables are rare. It seems that monkeys perceive spectral–temporal relations of multiple sounds to some extent. Japanese monkeys have been found to perceive frequency up-and-down patterns (Izumi, 2001, 2002). A similar perception of relative pitch has been observed in birds (e.g., Hulse et al., 1984) and dolphins (Ralston and Herman, 1995), and is prominent in humans from

the early stages of development (Demany and Armand, 1984; Trehub et al., 1984, 1987; Chang and Trehub, 1977). Furthermore, monkeys perceptually segregate tone sequences based on frequency proximity, and they perceive relative characters of the segregated stream as humans do (Izumi, 2002). These results have suggested that humans and other species have similar processes of perceptual organization.

Nevertheless, the processes of auditory organization in nonhumans may differ in certain ways from that in humans. Unlike humans, monkeys show strong preference for absolute rather than relative cues. D'Amato and Salmon (D'Amato and Salmon, 1982, 1984; D'Amato, 1988) tested perception of melody contours with Cebus monkeys, and concluded that monkeys discriminated melodies by local cues (absolute pitch of component tones) rather than by frequency contours. Similarly, macaque monkeys were shown to detect frequency-modulated tones by absolute-pitch cues rather than by the presence of modulation (Moody et al., 1986; Moody and Stebbins, 1989). Monkeys certainly perceive relative pitch, but they seem to prefer using absolute cues when available (Izumi, 2001).

In the present study, Japanese monkeys were trained to discriminate simplified spectral–temporal relation-

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ships to examine the robustness of relative pitch perception in monkeys. The stimuli used were pairs of pure tones whose frequencies were different, and the tones were presented sequentially. A silent gap was either inserted between the tones or not. The monkeys were required to discriminate whether the frequency of the second tone was higher or lower than the first tone. To succeed in this task, the monkeys had to perceive the relationship between the two tones. If the properties of auditory organization in monkeys are somewhat different from those in humans and the perception of relations in monkeys is relatively weak, the temporal separation of component tones would destroy such relative perception in monkeys.

2. Materials and methods

2.1. Subjects

The subjects were two male Japanese monkeys (*Macaca fuscata*; monkey 1: 8 years old; monkey 2: 5 years old). The use of the monkeys adhered to the Guide for the Care and Use of Laboratory Primates (1986) of the Primate Research Institute, Kyoto University. They were housed in individual cages with water freely available. The monkeys were previously trained to discriminate the frequency contours of tone sequences (Izumi, 2001, 2002). For comparison, seven humans participated in experiment 1. Four were female and three were males, with ages ranging between 23 and 29. They did not receive professional music training and did not report absolute pitch.

2.2. Apparatus

The tests were carried out in a sound-attenuating chamber (RE-246A, Tracoustics). Fig. 1 shows a schematic representation of the apparatus. A speaker, a lever, and a food tray that was connected to a universal feeder (UF-100, Davis Scientific Instruments) were placed on one side of the experimental box (50 cm wide \times 60 cm deep \times 70 cm high) in the chamber. A 15" computer monitor was placed above the speaker. A personal computer generated auditory stimuli with a sound card (Audiomedia III, Digidesign). The stimuli were prepared with 16-bit precision and a 22.05-kHz sampling rate. They were band-pass filtered between 100 and 5000 Hz (Model 3624, NF Electronics), amplified (AT-MA55, Audio-Technica) and presented via the speaker. The auditory stimulus level was calibrated with a sound level meter (NA-42, Rion) and a microphone (UC-53A, Rion) placed at the position of the monkey's head. The computer controlled the experimental procedure and data collection using a customized program.

2.3. Stimuli

The stimuli used were pairs of pure tones of different frequencies that were presented sequentially. Tone durations were different under each experimental condition, and included 5-ms rise–fall times (linear ramp). The tone intensity was approximately 70 dB SPL. There were rising and falling stimuli, and the frequency of the second tone was higher or lower than that of the first tone for the rising and falling stimuli, respectively. The frequencies of tones corresponded to that in the equal-tempered scale, and the frequency of the lower tone for each pair was 440, 494, 554, 622, or 698 Hz. For each pair, the interval sizes of the two tones were four semitones (i.e., 1/3 octave, approximately 26% difference in frequencies). The audiograms of both humans and monkeys were generally flat around these frequencies, and the sound level was well above the auditory thresholds (e.g., Jackson et al., 1999).

Fig. 2 shows a schematic representation of the stimulus used in experiment 1. The two tones comprising a stimulus were identical in duration. In training sessions, the duration of each tone was 400 ms, and the two tones were presented continuously (i.e., without a silent interval between the tones). In test sessions, discriminations were generalized to novel tone durations. Novel durations were 25, 50, 100, 200, and 300 ms for monkeys, and 10, 25, and 50 ms for humans. Although discriminating tone frequencies becomes more difficult with a decrease in tone durations, both humans and monkeys were expected to be able to easily discriminate the pitches of the two tones in the stimuli (see Sinnott and Brown, 1993). Tone durations were fixed in each trial. Test sessions contained trials in both the continuous and the gap conditions. For the continuous condition, two tones were presented continuously, as during training. For the gap condition, onset–onset asynchrony was fixed at 400 ms. That is, the onsets of consecutive tones were separated by 400 ms, and there was a temporal gap (i.e., silence) between tones because tone durations were less than 400 ms. Gap duration was 400 ms minus tone duration. Under the continuous condition, onset–onset asynchrony was the duration of the component tones.

The stimulus set in experiment 2 was designed to separate the positions of frequency transition and the temporal gap. In experiment 1, the position of the temporal gap was always at the frequency transition (i.e., there was a silent interval between the two tones), and it would not be concluded whether the effect of gap insertion depended on the temporal position of the gap. In other words, there was a possibility that the effect of gap insertion may have been different when the gap was at the frequency transition than when it was not. If a gap insertion were to have an effect only when the gap

was between two tones, it would be related to the perception of relations between tones. In this case, gap insertion between tones would eliminate local frequency transitions and the lack of sudden frequency transition would make discrimination difficult for monkeys. On the other hand, if gap insertion at any position in the stimuli were to affect the discrimination, other explanations would be possible. For example, monkeys may have failed to generalize their discrimination to novel stimuli with gaps because they were initially trained to discriminate stimuli without gaps.

Fig. 3 shows schematic representations of the stimuli in experiment 2. The stimuli were defined by three gap conditions and two transition positions, and there were six stimulus conditions used. The gap conditions included *no-gap*, *earlier-gap*, and *later-gap* conditions. For the *earlier-* and *later-gap* conditions, a 200-ms gap was inserted at 100 ms or 200 ms after the onset of the stimuli, respectively. The transition conditions included *earlier-* and *later-transition* conditions. A 100-ms tone was followed by a 400-ms tone for the *no-gap* and *earlier-transition* conditions, and vice versa for the *no-gap* and *later-transition* condition. For the *earlier-gap earlier-transition* and *later-gap later-transition* conditions, gaps were inserted at the frequency transitions, and these two conditions were designed as *match* conditions. For the *earlier-gap later-transition* and *later-gap earlier-transition* conditions, gaps were not at the frequency transitions, and the conditions were designed as *nonmatch* conditions. In these *nonmatch* conditions, the frequencies of the pregap and postgap tones were the same. The performance of the monkeys in the *match* conditions was predicted to be worse than in the *nonmatch* conditions if monkeys have limitations in the perception of relations between tones.

2.4. Procedure

2.4.1. Procedure for monkeys

A go/no-go procedure was used with positive reinforcement operant conditioning. The computer monitor lighted up in green, which cued the monkey to press the lever. When the monkey pressed the lever, the color of the monitor changed to red, and a trial began. After 0.5 s, a rising stimulus was presented as a sample stimulus. A comparison stimulus was either a rising or a falling stimulus, and it was presented 3 s after the onset of the sample stimulus. To make the monkeys attend to cues other than the absolute frequency of a component tone, stimuli were transposed for each presentation (i.e., tone frequencies were randomly selected from the five frequency sets for each presentation). The monkey was required to release the lever when a falling stimulus was presented as a comparison stimulus. The observation period was 3 s from the onset of the comparison

stimulus, and the response during this period was recorded. In trials with falling comparison stimuli, a response during the observation period was rewarded immediately with a small piece of sweet potato or a pellet food. In trials with rising comparison stimuli, the presentation of a falling stimulus followed the observation period. A response within 3 s from the onset of this follow-up stimulus was also rewarded. Responses outside these periods were not rewarded. An intertrial interval (ITI) of 3 s followed each trial. During each ITI, the computer monitor was darkened. Lever pressing during the interval was mildly punished by resetting the ITI. A trial was repeated after the ITI if the monkey released the lever before the observation period. There were the same numbers of trials with rising and falling comparison stimuli in each session. The percentage of correct response for each stimulus condition in a session was the arithmetic mean of the percentage of responses to falling comparison stimuli and the percentage of no responses to rising comparison stimuli.

In experiment 1, a session consisted of 132 trials, and each monkey had three sessions per day. Before the test sessions, the monkeys were required to perform above 70% percent correct in two consecutive sessions. Each monkey completed 15 test sessions. After the monkeys completed experiment 1, they immediately proceeded to experiment 2. In experiment 2, a session consisted of 108 trials, and each monkey had three sessions per day. The initial six sessions were the habituation phase,

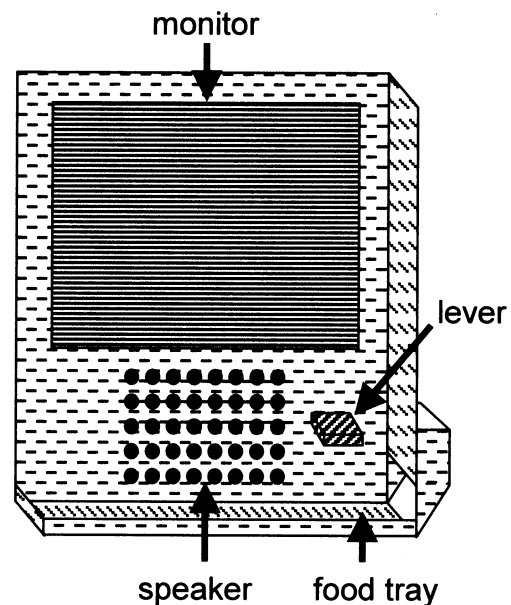


Fig. 1. Illustration of the front panel of the experiment box. The panel was attached to one side of the experiment box in a sound-attenuating chamber. This panel contained a lever for monkey's responses, a speaker and a monitor for auditory and visual stimulus presentations, and a feeding tray connected to an automatic feeder.

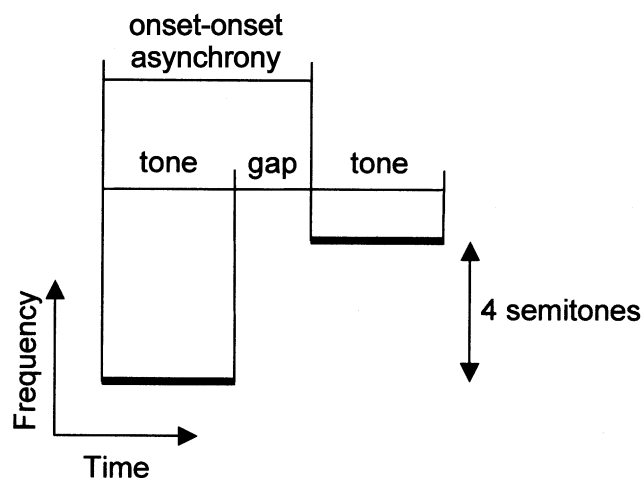


Fig. 2. Schematic representation of the stimuli in experiment 1. Two thick lines represent component tones. As shown, the stimulus is a rising stimulus when the second tone is higher in frequency. Two tones were separated by four semitones in frequency. For the continuous condition, there was no temporal gap and the onset–onset asynchrony was equal to the tone duration. For the gap condition, onset–onset asynchrony was fixed at 400 ms, and gap duration was 400 ms–tone duration.

and the data from the following 15 sessions were used for analysis.

2.4.2. Procedure for humans

The procedure for the human participants was generally similar to that for the monkeys. Before the session, the participants were instructed to press the lever and to release it when they heard falling stimuli. Correct responses by humans were not rewarded with food, but feeder clicks were given. A session consisted of 120 trials, and each participant had only one session.

3. Results

3.1. Experiment 1

Fig. 4 shows the percentage of correct responses of the two monkeys and the human participants. For the human participants, the performance under the gap condition was superior to that under the continuous conditions ($P < 0.0005$, signed rank sum test). The performance deteriorated with the decrease in tone duration under the continuous condition ($P < 0.005$, Friedman test), but not under the gap condition. These results for humans can be explained by the temporal discriminability of onset–onset asynchrony of two tones. Under the gap condition, onset–onset asynchrony was fixed at 400 ms. Under the continuous condition, however, onset–onset asynchrony was the duration of component tones and was shortened with the

decrease in tone durations. Human performance appeared to decline with the decrement of onset–onset asynchrony.

Both monkeys reached the performance criterion within nine training sessions. The trends in the data of the two monkeys were similar in the test sessions. Regardless of easier acoustical parameters for the discrimination, the performance of monkeys was generally lower than that of humans. Humans show remarkably superior performance compared to monkeys in frequency and temporal discrimination (frequency discrimination: e.g., Sinnott et al., 1985; temporal discrimination: Sinnott et al., 1987; Izumi, 1999), and this seemed to be a reason of the performance differences in the present study. A two-way analysis of variance (ANOVA; gap presence/absence \times tone duration) was carried out for each monkey's performance. The performance was worse under the gap condition [monkey 1: $F_{(1,19)} = 27.43$, $P < 0.0001$; monkey 2: $F_{(1,19)} = 14.28$, $P < 0.005$] and the conditions with shorter durations [monkey 1: $F_{(4,76)} = 10.23$, $P < 0.0001$; monkey 2: $F_{(4,76)} = 19.97$, $P < 0.0001$]. Interaction was significant in monkey 1 [$F_{(4,76)} = 3.08$, $P < 0.05$], but not in monkey 2 [$F_{(4,76)} = 2.43$, *ns*]. The deterioration of the performance of the monkeys with the decrease in tone duration under the continuous condition was similar to that of the human participants, and was interpreted as a result of temporal discriminability. Shorter onset–onset asynchrony appeared to make discrimination difficult for monkeys as well as for humans. The performance deterioration in the monkeys with the insertion of gaps was not observed in the human participants, and tem-

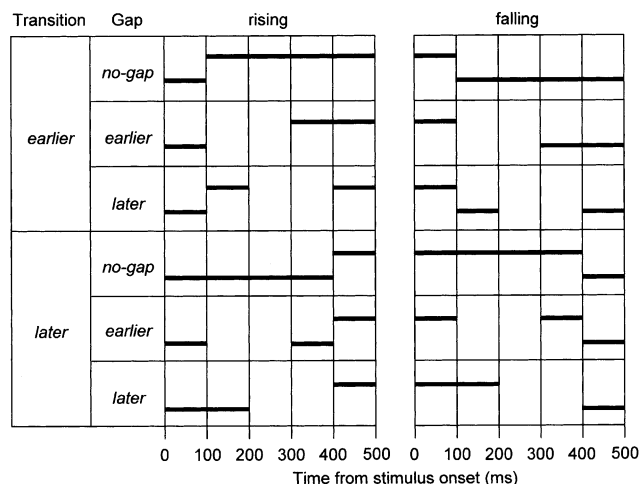


Fig. 3. Schematic representations of the stimuli in experiment 2. Two or three thick lines represent component tones in each condition. For the *earlier-gap earlier-transition* and *later-gap later-transition* conditions, 200-ms gaps were inserted at the frequency transitions (*match* conditions). For the *earlier-gap later-transition* and *later-gap earlier-transition* conditions, gaps were not at the frequency transitions (*nonmatch* conditions).

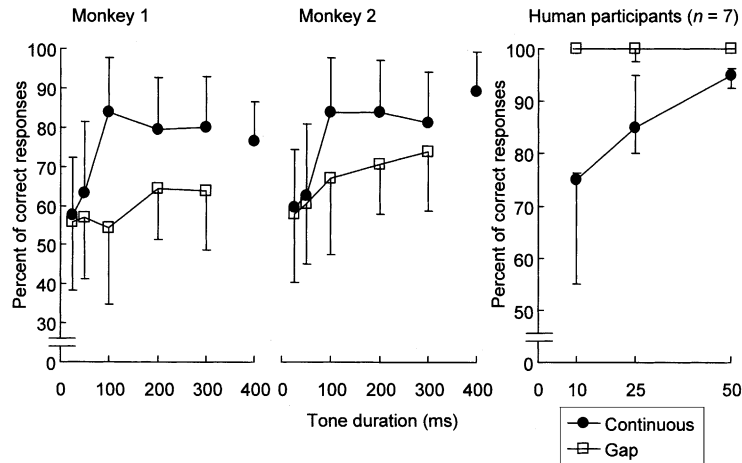


Fig. 4. Percentage of correct responses for monkeys and humans in experiment 1. For monkeys, plots represent averages, and error bars are standard deviations. Data for the human participants are the medians of seven participants, and error bars are quartile deviations.

poral discriminability cannot explain these results. These results were in accord with the idea that the processes of auditory organization in monkeys are somewhat different from those in humans, and monkeys perceive relative relations of tones under limited conditions.

The performance decrement in monkeys with the insertion of gaps could be discussed with respect to short-term memory. In the gap condition, monkeys had to remember the pitch of the first tone during the silent interval between the tones to compare the pitches of the two tones. Auditory memory, however, did not seem to fully explain the present results. The shortest gap in the present study was 100 ms (tone duration of 300 ms), and even this gap lowered the performance of monkeys. Although monkeys show less robust auditory memory compared to auditory and visual memory in humans and visual memory in monkeys, their retentions are reasonably accurate for several seconds (Kojima, 1985; Colombo and D'Amato, 1986). Furthermore, if performance was restricted by memory, it would have decreased gradually with the elongation of the retention time (here the duration of the silent interval). In practice the performance suddenly decreased by the insertion of the shortest gap, and was relatively stable in the gap condition with various gap durations.

3.2. Experiment 2

Fig. 5 shows the percentage of correct responses for each monkey. A two-way ANOVA (gap condition \times transition position) was carried out for each monkey. For monkey 1, there was no significant main effect, but the interaction was significant [$F_{(2,38)} = 20.40$, $P < 0.0001$]. For the *earlier-gap* conditions, the monkeys showed better performance under the *later-transition* condition than under the *earlier-transition* condition

[monkey 1: $F_{(1,57)} = 20.95$, $P < 0.001$; monkey 2: $F_{(1,57)} = 46.13$, $P < 0.0001$]. Under the *later-gap* conditions, however, the performance of the monkeys was better under the *earlier-transition* condition than under the *later-transition* condition [monkey 1: $F_{(1,57)} = 17.90$, $P < 0.0001$; monkey 2: $F_{(1,57)} = 9.78$, $P < 0.005$]. That is, the performance of the monkeys was worse in *match* conditions in which the gaps were inserted at the frequency transitions. This means that the discriminations of monkeys depended on the frequency transitions, and the replacement of frequency transitions with silences made discrimination difficult.

4. Discussion

Perhaps partly due to superior spectral and temporal discriminability in humans compared to monkeys (fre-

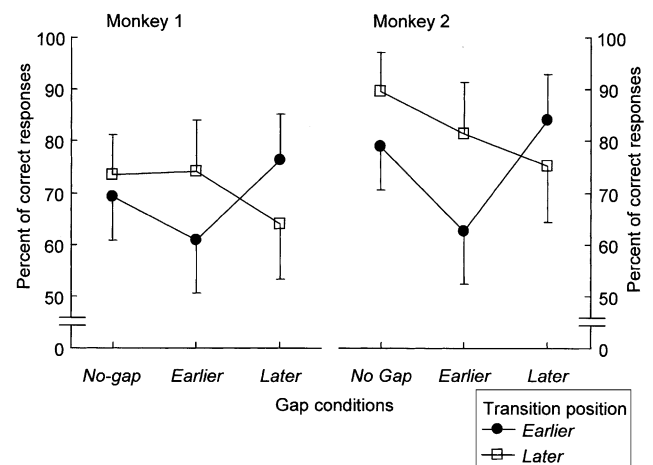


Fig. 5. Mean percentage of correct responses for each monkey in experiment 2. Parameters are transition positions. Error bars represent standard deviations.

quency discrimination: e.g., Sinnott et al., 1985; temporal discrimination: Sinnott et al., 1987; Izumi, 1999), absolute performances of the human participants were superior to those of the monkeys in the present study. Marked differences in absolute performance sometimes make it difficult to directly compare performance trends. However, performance trends for the human participants and the monkeys were quite different in experiment 1, and the frequency and temporal discriminability did not explain this difference. The monkeys showed difficulty in perceiving the relationship of two tones when a gap was inserted between tones, but the human participants did not. From the results of experiment 2, the monkeys' performance deterioration with the insertion of gaps was explained as a result of the elimination of local frequency transitions. Such perceptual characteristics of monkeys seem very different from those of humans.

The present results suggested that monkeys pay more attention to local cues than humans do in perceiving tone sequences. In other words, humans use global cues more extensively than monkeys do. Relative global dominance in humans is manifested in the visual modality. Compared to chimpanzees (*Pan troglodytes*), baboons (*Papio papio*), rhesus monkeys (*Macaca mulatta*), and pigeons (*Columba livia*), humans show advantages of global processing in perceiving visual hierarchical stimuli (Fagot and Deruelle, 1997; Deruelle and Fagot, 1998; Fagot and Tomonaga, 1999; Cavoto and Cook, 2001; Hopkins and Washburn, 2002). In these studies, the stimuli used consisted of small shapes (i.e., local elements) that were arranged to form global shapes. Generally, humans showed advantages of processing global shapes, but nonhumans showed local advantages. Another study on the perception of Kanizsa-square illusory figures (one type of the perception of illusory contour) revealed that chimpanzees' perception of the illusory contour is more easily affected by the separation between visual elements than humans' (Fagot and Tomonaga, 2001). This may relate to the relative weakness of global perception in chimpanzee vision.

The results of the previous investigation on relative pitch perception implied the limited use of relative cues in monkeys' auditory perception (Izumi, 2001). Japanese monkeys were initially trained to detect changes from rising to falling contours of three-tone sequences, and they were able to transfer relative pitch perception to novel sequences within the absolute frequency range of the training phase, but such perception did not transfer to sequences outside the training range. Similar results were also shown in birds (e.g., Hulse et al., 1984). Furthermore, D'Amato and Salmon (D'Amato and Salmon, 1982, 1984; D'Amato, 1988) failed to demonstrate relative pitch perception in monkeys because monkeys persisted to use absolute pitches of component

tones in discriminating tone sequences. In the present study, the performance deterioration with the insertion of a temporal gap was not because the monkeys attended to the absolute pitches of the component tones. Rather, monkeys attended to the local frequency transition between the two tones. Together with the previous results concerning relative pitch perception, monkeys' performances may well be explained based on aspects of global/local processing.

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