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H. Riquimaroux, T. Hashikawa. Units in the primary auditory cortex of the Japanese monkey can demonstrate a conversion of temporal and place pitch in the central auditory system. Journal de Physique IV Proceedings, 1994, 04 (C5), pp.C5-419-C5-425. 10.1051/jp4:1994588 . jpa-00253083

HAL Id: jpa-00253083

<https://hal.science/jpa-00253083>

Submitted on 1 Jan 1994

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Units in the primary auditory cortex of the Japanese monkey can demonstrate a conversion of temporal and place pitch in the central auditory system

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Abstract

The present study has examined whether the temporal pitch known as the “missing fundamental” is co-place-coded with the place pitch in the auditory cortex, using adult Japanese monkeys (*Macaca fuscata*) prepared for chronic recordings. The stimuli were white noise bursts, tone bursts and bursts of a combination of higher harmonics of a low frequency. Unit recordings were made from the contralateral (left) primary auditory cortex (AI). During recording sessions, the animal was anesthetized with a mixture of nitrous oxide and oxygen, supplemented by ketamine and xylazine injections. The data have confirmed a tonotopicity, low frequency anteriorly while high frequency posteriorly, in AI when the recording time window was short (< 20 msec) with stimulus at threshold levels. For longer time windows and/or suprathreshold stimulus levels, determining the best frequency (BF) for a neuron was often difficult. In the low frequency area (≤ 500 Hz), the same neuron responded to BF as well as a combination of successive higher harmonics of BF without BF. However, they did not or little responded to the harmonics themselves. The findings imply that the temporally-coded pitch at the periphery appears to be already place-coded together with the place pitch by the same neuron at AI. This evidence agrees well with previous psychoacoustical findings.

1. INTRODUCTION

Since 19th century, it is a well known fact in psychoacoustics that the ear sometimes perceives tones which do not correspond to any of the Fourier-components of the objective sound [1,2]. When we add several higher harmonics, we have a pitch sensation of the low-frequency fundamental which does not exist in the sound (called the “missing fundamental” or “virtual pitch”, Fig. 1). Although the phase-locked firing corresponding to the virtual pitch exists in the temporal discharge pattern of the cochlear nerve fibers [3], it has been believed that the missing fundamental pitch is extracted not by the peripheral but by the central auditory system [4]. The missing fundamental pitch sensation cannot be masked by a low-pass noise. If it is originated in the cochlea, it should be masked by the low-pass noise. The missing fundamental sensation can be created by a dichotic presentation of harmonics from each ear [5]. If it is

created by the peripheral auditory system, the dichotic stimulation with harmonics would not produce the missing fundamental pitch. However, little is neurophysiologically investigated about this problem. This study examined whether the place pitch (fundamental frequency, f_0) and the temporal pitch (missing fundamental) are co-place-coded by the same neuron at the level of primary auditory cortex (AI).

2. METHODS

2.1 Subjects

Adult Japanese monkeys (*Macaca fuscata*) were used for this study. After an otoscopic examination, they were screened with the auditory brainstem responses (ABR) and slow cortical responses (SVR) before surgical procedure. A monkey with poor ABR or SVR was rejected from the experiment.

2.2 Surgical procedure

All surgeries were aseptically performed with sufficient anesthesia by means of an intravenous injection of a mixture of ketamine and xylazine. After cleaning the skull, a metal post was glued at the vertex. A temporal portion of the skull was removed in round shape over which a chamber (diameter = 3 cm) was placed for chronic recordings. The dura remained intact. Recordings started 2 weeks after the surgery. Intramuscular injections of antibiotics for 7 days and topical application of antibiotics to the surgically wounded area prevented infections.

Fig. 1 A combination of four higher harmonics to produce the "missing fundamental". A: 1000, 1200, 1400 and 1600 Hz sinusoidal signals (pure tones) are illustrated in a, b, c and d, respectively. B: Temporal wave pattern produced by adding 1000, 1200, 1400 and 1600 Hz. A periodicity of 5 ms, corresponding to 200 Hz, is visible. C: Power spectrum of the synthesized wave shown in B. Peaks for 1000, 1200, 1400 and 1600 Hz can be observed but no peak for the missing fundamental (200 Hz, broken line).

2.3 Stimulus

The stimuli used were white noise bursts, tone bursts and bursts of a combination of higher harmonics of a low fundamental frequency (f_0). White noise was digitally generated by a random noise generator (NF,WG-721A). Sinusoidal waves were also digitally generated by an arbitrary waveform generator (Yokogawa, AG-1200). Continuous white noise and sinusoidal waves were passed through a tone-burst modulator (DIA Medical, DPS-721) to make burst stimuli. The stimulus was attenuated (Tamagawa, TPA-308A), amplified (Sony, TA-N7050) and then presented by a loud speaker to the animal's right ear which was located 25 cm from the speaker. The left external ear canal was occluded by an ear plug. The sound stimulus was monitored through a microphone located at the place where the animal's ear was placed with a measuring amplifier (ACO, 6030) and an FFT analyzer (Advantest, R9211B). Rise/fall time was 10 msec and the plateau was fixed at 20 msec, making total duration of 40 msec. The stimulus was presented once every 3 sec. Frequency varied from 100 Hz to 25 kHz. The stimulus intensity was changed from the neuron's threshold to 70 dB SPL for tone bursts and to 90 dB SPL for white noise bursts. The sound pressure level was measured with continuous tones and white noise because the RMS meter could not follow the envelope of burst stimuli. The white noise burst was used to search auditory units.

2.4 Recordings

The animal was put on a stage in an electromagnetically shielded sound proof room. The head was immobilized by fixing the metal post on the skull to a hollowed metal rod with a screw. Unit recordings were made with glass-coated Elgiloy electrodes from the left primary auditory cortex (AI) on the superior temporal plane (**Fig. 2A**). During recording sessions, the animal was anesthetized with a mixture of nitrous oxide and oxygen, supplemented by ketamine and xylazine injections. Body temperature was maintained at 38°C. The heart rate was monitored (Nihonkoden, AC-611G) throughout the experiment. The electrode was tilted by 55° from the horizontal plane and orthogonal to the anterior-posterior line. The electrode was advanced by a pulse-motor micromanipulator (Narishige, custom-made). Cortical activities were filtered (300 Hz - 3 kHz), amplified (Nihonkoden, AB-651J) and fed into a window discriminator (DIA Medical, DSE-435) to produce a pulse corresponding to a neural action potential, which was sent to a computer (NEC, PC-9801DA) to generate PST (post-stimulus-time) histograms on line. Twenty trials were usually summed to create one PST histogram. The PST histogram was triggered 30 msec prior to the stimulus onset and continued for 350 msec (**Fig. 3**). The minimum bin width of the PST histogram was 1 msec. Recordings were made once a week for each animal. After each recording session, the chamber was cleaned and sealed for the next experiment.

2.5 Neuroanatomy

After finishing all the recordings, the animal was sacrificed by a lethal dose of pentobarbital, followed by a perfusion through the heart with saline and then 4% paraformaldehyde in phosphate buffer. Immediately after the perfusion, the brain was taken out and immersed in a sucrose solution. Nissl and parvalbumin stainings were made with 30 μ m sections, in which the primary auditory cortex was identified as the koniocortex [6]. Then, the recording sites were examined. Parvalbumin staining shows AI [7].

3. RESULTS

We confirmed that our recordings were made from AI by comparing a Nissl staining containing electrode tracks with a parvalbumin staining indicating AI (Fig. 2). The darkly stained area of within the lateral sulcus (LS) in Fig. 2c indicates AI [7]. Tonotopicity was found in antero-posterior direction. Low frequency neurons (≤ 500 Hz),

Fig. 2 Frontal sections showing recording sites. **A:** A schematic electrode track is illustrated. electr: electrode, LS: lateral sulcus, STS: superior temporal sulcus, TH: thalamus. **B:** Nissl staining of a recording site (outlined by broken line in A) showing electrode tracks (arrow head). **C:** Parvalbumin staining of a recording site (outlined by broken line in A). Darkly stained area indicates the primary auditory cortex. Bars indicate 5 mm in A and 3 mm in B and C.

Fig. 3 Typical responses of low frequency neurons to the fundamental frequency (fo), the combination of higher harmonics without the fo and each higher harmonic component. **A, top row:** from left responses to 200 Hz, a complex of 2.0k + 2.2k + 2.4k + 2.6kHz and control condition, respectively. **bottom row:** responses to 2.0 kHz, 2.2 kHz, 2.4 kHz and 2.6 kHz, respectively. BF = 200 Hz, Intensity = 60 dB SPL (each frequency component of the complex sound is 48 dB SPL). **B, top row:** responses to a complex of 2.0k + 2.5k + 3.0k + 3.5 kHz, 2.0 kHz, 3.5 kHz and 500 Hz, respectively. **middle row:** responses to a complex of 5.0k + 5.5k + 6.0k + 6.5kHz, 5.0 kHz, 6.5 kHz and control condition, respectively. **bottom row:** responses to a complex of 10.0k + 10.5k + 11.0k + 11.5kHz, 10.0 kHz and 11.5 kHz, respectively. BF = 500 Hz, Intensity = 70 dB SPL (each frequency component of the complex sound is 58 dB SPL). **C, first row:** responses to a complex of 800 + 1.0k + 1.2k + 1.4 kHz, 800 Hz, 1.0 kHz, 1.2 kHz and 1.4 kHz, respectively. **second row:** responses to a complex of 2.0k + 2.2k + 2.4k + 2.6 kHz, 2.0 kHz, 2.2 kHz, 2.4 kHz and 2.6 kHz, respectively. **third row:** responses to a complex of 4.0k + 4.2k + 4.4k + 4.6 kHz, 4.0 kHz, 4.2 kHz, 4.4 kHz and 4.6 kHz, respectively. **fourth row:** response to 200 Hz and control condition. BF = 200 Hz, Intensity = 70 dB SPL (each frequency component of the complex sound is 58 dB SPL).

located in the anterior part of AI, were characterized to examine the conversion of the place pitch and the temporal pitch produced by a combination of four higher harmonics without the fo (**Fig. 1**). All of 15 neurons examined responded to the fo as well as a combination of higher harmonics without the fo. However, they did not or little responded to each higher harmonic component (**Fig. 3ABC**). Moreover, they only responded to a combination of higher harmonics in a certain frequency range (**Fig. 3BC**).

4. SUMMARY and DISCUSSION

In the low frequency area (≤ 500 Hz), a single neuron responds both to the best frequency (BF) and to a combination of successive higher harmonics which creates a temporal periodicity identical to the BF (**Fig. 1**), but not to these higher harmonic components themselves (**Fig. 3ABC**). Further, the higher harmonics have to be within a certain frequency range for the combined harmonics to produce the same pitch as the fo (**Fig. 3BC**). Thus, not only the periodicity created by the harmonics but also the actual frequency of the harmonics appear to be important for the missing fundamental pitch extraction. This tendency is similar to previous human psychoacoustical findings [1, 2, 8] (**Fig. 4**). For example, **Fig. 4** indicates that human subjects can perceive the missing fundamental pitch of 100 Hz only when the lowest harmonic frequency is between 500 Hz and 2 kHz [8]. Human lesion studies have also shown data agree with the present findings. Namely, patients without AI have difficulties to perceive the missing fundamental pitch but that patients with temporal lobectomy with an intact AI show a normal missing fundamental sensation [9, 10]. A recent auditory-evoked magnetic field study has implied that a combination of higher harmonics without the fo and the fo are processed in the same area in the auditory cortex of humans [11], which also agrees with the present results. Schwarz and Tomlinson [12] failed find neurons in the auditory cortex of the rhesus monkey which responded to the fo as well as the combination of higher harmonics without the fo. The reason why they could not find

Fig. 4 Region where the missing fundamental pitch exists. Fundamental frequency as a function of the lowest component in the higher harmonic complex. Shaded area: region where the missing fundamental exists. Broken line: fundamental frequency. (from Zwicker and Fastl, 1990)

such neurons, which we have described here, is not clear. The present data suggest that the temporally-coded pitch in the periphery appears to be already place-coded together with the place pitch by the same neuron to produce an identical pitch at AI. Experiments with a low-pass masker with the missing fundamental situation, a dichotic presentation of harmonics from each ear and an inharmonic combination of frequency components with a constant spacing frequency will be interesting tests to examine the central processing of the missing fundamental pitch extraction.

acknowledgement

The authors show gratitude to Dr. E. G. Jones for his help to conduct this study. The research was supported by Frontier Research Program, RIKEN.

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