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Neural mechanisms of the octave illusion: electrophysiological evidence for central origin

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THE octave illusion is experienced when two simultaneous tones, separated by one octave and presented to the opposite ears, are continuously reversed between the two ears. Subjects consistently report a sequence of alternating single tones: the high tone in the right ear and the low in the left. We wished to determine whether such a complex tone sequence is encoded as it is presented or as it is perceived. This was accomplished by making the tone sequence infrequently correspond to how it is perceived, and recording event-related potentials (ERPs) to these perceptually equivalent but physically different events. The illusion-mimicking tones elicited the mismatch negativity (MMN), a change-specific ERP component with origin in the auditory cortex. This indicates that the stimuli giving rise to the octave illusion are encoded according to their physical rather than perceptual properties. Consequently, the generator of the octave illusion is located beyond the level of the auditory cortex.

Key words: Audition; Human; Mismatch negativity; Octave illusion; Pitch perception; Sensory memory

Introduction

Pitch perception does not necessarily correspond to the spectral contents of a complex tone.[1,2] This discrepancy may give rise to a number of auditory illusions.[3,4] For example, the octave illusion[5–8] is experienced when two tones with frequencies separated by a full octave (e.g. tones of 400 and 800 Hz) are presented simultaneously to the opposite ears, so that the low and the high tone continuously reverse their positions between the two ears (Fig. 1a). Under such conditions, subjects tend to perceive only one tone at a time instead of two tones. Right-handed subjects mostly report the high tone in the right ear, when this tone was actually presented to the right ear and the low tone to the left ear, and they report the low tone in the left ear when it was presented to the right ear and the high tone to the left ear (Fig. 1b). Left-handed subjects do not localize the tones preferentially either way.[5]

The neural basis of such auditory illusory perception can be studied by recording event-related brain potentials (ERPs), and particularly by measuring the mismatch negativity (MMN) component of the ERPs.[9] The MMN is elicited by any discriminable change in auditory stimulation (e.g. by a change in tone frequency or duration) even if the subject concentrates on performing a task unrelated to the stimulation.[10] Its occurrence reflects a result of a preattentive comparison process where a neural representation of a frequently presented auditory stimulus event and new sensory input with a different sensory information content are found to be discrepant (mismatching). This implies that the information of the frequently presented stimulus event has been encoded by the auditory system in the form of some neural representation. The main contribution to the MMN generation results from the activity of the auditory cortex.[11–14] Despite the pre-attentive nature of MMN, its occurrence seems to predict the subject's performance in attentive stimulus discrimination tasks.[15]

The present study addressed the question of whether the stimuli eliciting the octave illusion are encoded by the central nervous system in terms of their physical (spectral) or perceptual (illusory) properties. In other words, are the stimuli mimicking the octave illusion (the tones spectrally corresponding to the illusory perception; represented in Fig. 1b) processed in the same way as the original tones eliciting the illusion (represented in Fig. 1a) or not? If yes, i.e. if occasional stimuli mimicking the illusion do not elicit MMN, then the octave illusion would have its neural locus below or at the level of MMN generation known mainly to occur in or near the primary auditory cortex.[11–14] If no, i.e. if occasional stimuli mimicking the illusion do elicit MMN, then one could conclude that the content of the memory traces does not correspond to the illusory perception and that, consequently, the neural substrate of the illusion should be sought for a level higher than the primary auditory cortex.

Materials and Methods

The frequently presented standard stimulus event in the present study was composed as follows. The two simultaneous short tones were one of 400 Hz presented to one ear and the other of 800 Hz presented to the other ear through headphones at about 75 dB SPL. This dichotic stimulus of 250 ms in duration was continuously repeated with 50 ms silent intervals so that the two tones alternated between the two ears (Fig. 1a). In the condition with Illusion-Consistent Deviant, a high tone was presented to the right ear followed by the low tone presented to the left ear (both tones presented with no parallel tone in the opposite ear; Fig. 1c). In the condition with the Illusion-Inconsistent Deviant, the high and low tones of the deviant event changed their order (Fig. 1d).

A total of 3000 dichotic tone pairs in both conditions were presented to subjects on a quiet low-pass noise background, in blocks of 500 tones. Each block consisted of 95% standard events and 5% deviant events. The order of the blocks was randomized across subjects. During the experiment, conducted in an acoustically and electrically shielded room, subjects were reading a self-selected book without paying attention to tones. After the experimental session, all subjects were interviewed. Nine subjects (three males and six females, all with reported normal hearing, one left-handed) of the total of 18 provided the expected illusory description of the standard stimuli. That is, they reported as having perceived an alternating sequence of single high and low tones, with the high tone lateralized in the right ear and the low tone in the left ear. The results of only these subjects will be reported in the present article.

The EEG (sampling rate 200 Hz; bandpass 0.1–100 Hz) was recorded with Ag–AgCl electrodes at 10 scalp locations with the nose as a reference: Fpz, Fz, Cz, and Pz at the midline, and six electrodes on the tilted coronary line from the mastoids to Fz, labelled L1, L2, and LM (the left mastoid) on the left and R1, R2, and RM (the right mastoid) on the right hemisphere. ERPs following standard and deviant stimuli were separately offline-averaged for individual subjects and thereafter digitally low-pass filtered (0.1–30 Hz). EEG epochs with voltage changes exceeding 100 μV were automatically omitted from further analysis. The grand-average ERPs were formed by averaging across ERPs of individual subjects. The MMN amplitude was measured from the individual subtraction waves obtained by subtracting the ERP to standard stimulus from that to the deviant stimulus, using a 20 ms integration window centred at the most negative peak in the grand-average subtraction wave at Fz.

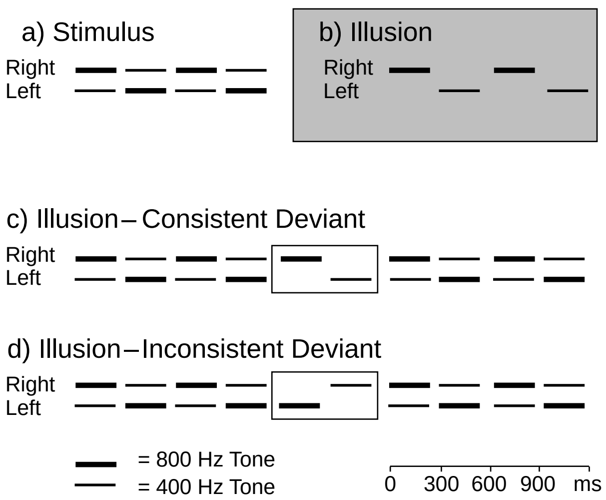

FIG. 1. Stimuli used in the experiment. (a) The standard event was a pair of successive dichotic complex sounds each consisting of two simultaneous pure tones: 400 Hz (thin line) and 800 Hz (thick line). In the first pair, the high tone was presented to the right ear and the low tone to the left ear. In the second pair, the high and the low tone were dichotically reversed, so that the low tone was fed to the right and the high tone to the left ear. (b) This sound sequence is frequently perceived by right-handed subjects as a string of alternating single high right-ear and low left-ear tones. (c) When Illusion-Consistent, the deviant event was a pair of successive single pure tones, the high tone (800 Hz) presented to the right ear and the low tone (400 Hz) presented to the left ear. (d) When Illusion-Inconsistent, the deviant event consisted of the high tone presented to the left ear and the low tone to the right ear.

Results and Discussion

The deviant events elicited MMN when they were illusion consistent as well as when they were illusion inconsistent (Fig. 2). Its peak latency was 155 ms from stimulus onset for the Illusion-Consistent and around 185 ms for the Illusion-Inconsistent Deviant events and at R1 electrode for the Illusion-Inconsistent Deviants.

The MMN was statistically significant at Fz and L1 for both deviant events (Table 1; $p < 0.05$, one-tailed t-test) and at R1 electrode for the illusion inconsistent deviants. The MMN reversed its polarity in mastoid electrodes, the polarity reversal being significant at RM and LM for the Illusion-Consistent Deviants and marginally significant at RM for the Illusion-Inconsistent Deviants. The polarity reversal observed suggests that the MMN generator is located in the auditory cortex. The MMN amplitudes did not differ statistically significantly between the two conditions (paired two-tailed t-test for Fz, L1, R1, LM, and RM).

The present data show that at the level of pre-attentive sensory processing, there are different representations for two stimulus categories which are identically perceived in terms of pitch and lateralization (i.e. standards and deviants in the condition in which deviants were consistent with the illusion).

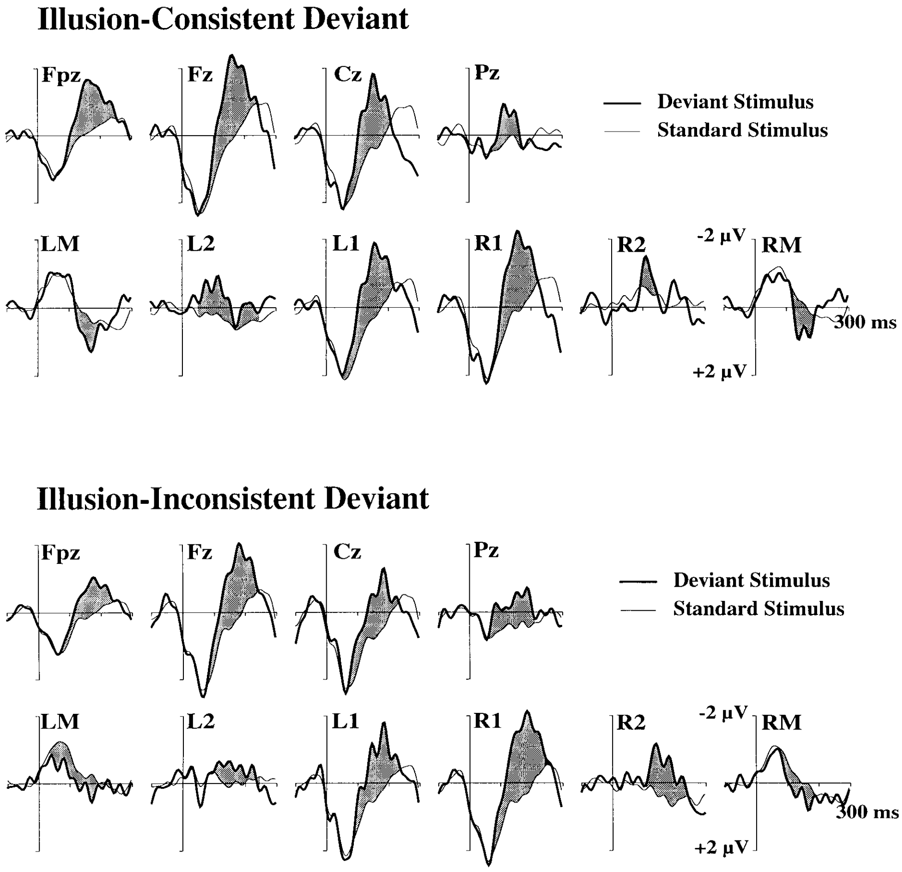

FIG. 2. The event-related potentials to standard (thin line) and deviant (thick line) stimuli when the deviants were Illusion-Consistent (upper panel) and Illusion-Inconsistent (lower panel). The dark area illustrates the change-specific mismatch negativity (MMN) component.

Table 1 The MMN mean amplitudes and their statistical significance (the standard deviation is given in parentheses).

Electrode	MMN amplitude (μV)	
	Illusion-Consistent Deviant	Illusion-Inconsistent Deviant
Fz	–1.97 (2.54)*	–1.57 (0.97)***
L1	–1.64 (2.02)*	–1.47 (1.16)**
R1	–1.60 (2.69)#	–1.79 (1.56)**
LM	0.83 (1.12)*	0.30 (0.95) n.s.
RM	0.88 (1.08)*	0.58 (1.25)#

The MMN amplitude was measured from the individual subtraction waves obtained by subtracting the ERP to standard stimulus from that to the deviant stimulus, using a 20 ms integration window centred at the most negative peak in the grand-average subtraction wave at Fz. $***p < 0.001$; $**p < 0.01$; $*p < 0.05$; $^{\#}p < 0.1$; n.s., not significant.

In addition, MMNs of very similar amplitudes were elicited by both deviant events, that is, irrespective of whether or not the deviant event replicated the reported illusory perception of the standard. This suggests that the auditory system creates the illusion from the original sound material beyond the level of the auditory cortex.

Conclusion

Two categories of auditory stimuli which have different spectral structure but which are identically perceived in terms of pitch and lateralization, are differently encoded on the level of sensory memory. This implies that the octave illusion is created by the central nervous system beyond the level of the auditory cortex.

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References

1. de Boer E. On the 'residue' and auditory pitch perception. In: Keidel WD and Neff WD, eds. *Handbook of Sensory Physiology*. Berlin: Springer, 1976: 479–583.
2. Scharf B and Houtsma AJM. Loudness, pitch, localization, aural distortion, pathology. In: Boff KR, Kaufman L and Thomas JP, eds. *Handbook of Perception and Human Performance*, Vol. 1. New York: Wiley, 1986, Chapter 15: 20–32.
3. Deutsch D. *Sci Am* 233, 92–104 (1975).
4. Wessel D and Risset JC. Les illusions auditives. In: Risset JC, ed. *Encyclopaedia Universalis*, Vol. 15. Paris, 1979: 167–171.
5. Deutsch D. *Nature* 251, 307–309 (1974).
6. Deutsch D. Auditory pattern recognition. In: Boff KR, Kaufman L and Thomas JP, eds. *Handbook of Perception and Human Performance*, Vol. 2. New York: Wiley, 1986, Chapter 32: 9–14.
7. Houtsma AJM, Rossing TD and Wagenaars WM. *Auditory Demonstrations*. Eindhoven: Institute for Perception Research, 1987: 91–92.
8. Deutsch D. *J Acoust Soc Am* 83, 365–369 (1988).
9. Näätänen R, Gaillard AWK and Mäntysalo S. *Acta Psychol* 42, 313–329 (1978).
10. Näätänen R. *Attention and Brain Function*. Hillsdale, NJ: Lawrence Erlbaum, 1992.
11. Hari R, Hämäläinen M, Ilmoniemi RJ *et al. Neurosci Lett* 50, 127–132 (1984).
12. Giard MH, Lavikainen J, Reinikainen K *et al. J Cognit Neurosci* 7, 133–143 (1995).
13. Winkler I, Tervaniemi M, Huotilainen M *et al. NeuroReport* 6, 2317–2320 (1995).
14. Kropotov JD, Näätänen R, Sevostianov AV *et al. Psychophysiology* 38, 418–422 (1995).
15. Tiitinen H, May P, Reinikainen K *et al. Nature*, 372, 90–94 (1994).

General Summary
The present study addresses the neural mechanism of the octave illusion. The auditory illusion is experienced when a sequence of high and low tones, by one octave apart, are simultaneously presented through the headphones, to the opposite ears so that they continuously reverse the ear of presentation. Subjects consistently report a sequence of alternating single tones: The high tone in the right and the low tone in the left. So there is discrepancy between the physical description of the sounds and their perception. We studied whether such a complex tone sequence is encoded by the central nervous system as it is presented or as it is perceived. This was accomplished by making the tone sequence infrequently correspond to how it is perceived, and recording event-related brain potentials (ERPs) to these perceptionally equivalent but physically different events. The change-specific MMN component, generated in the auditory cortex, was elicited by the illusion-mimicking tones indicating that the central nervous system encode the present stimuli rather in terms of physical than perceptual properties. Consequently, the generator of the octave illusion is beyond the level of the auditory cortex.