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Research Paper

Neural correlates of auditory scale illusion

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ABSTRACT

The auditory illusory perception “scale illusion” occurs when ascending and descending musical scale tones are delivered in a dichotic manner, such that the higher or lower tone at each instant is presented alternately to the right and left ears. Resulting tone sequences have a zigzag pitch in one ear and the reversed (zagzig) pitch in the other ear. Most listeners hear illusory smooth pitch sequences of up-down and down-up streams in the two ears separated in higher and lower halves of the scale. Although many behavioral studies have been conducted, how and where in the brain the illusory percept is formed have not been elucidated. In this study, we conducted functional magnetic resonance imaging using sequential tones that induced scale illusion (ILL) and those that mimicked the percept of scale illusion (PCP), and we compared the activation responses evoked by those stimuli by region-of-interest analysis. We examined the effects of adaptation, i.e., the attenuation of response that occurs when close-frequency sounds are repeated, which might interfere with the changes in activation by the illusion process. Results of the activation difference of the two stimuli, measured at varied tempi of tone presentation, in the superior temporal auditory cortex were not explained by adaptation. Instead, excess activation of the ILL stimulus from the PCP stimulus at moderate tempi (83 and 126 bpm) was significant in the posterior auditory cortex with rightward superiority, while significant prefrontal activation was dominant at the highest tempo (245 bpm). We suggest that the area of the planum temporale posterior to the primary auditory cortex is mainly involved in the illusion formation, and that the illusion-related process is strongly dependent on the rate of tone presentation.

1. Introduction

Scale illusion is an illusory perception of auditory sounds that are delivered to listeners' right and left ears in distinctive tone sequences. The stimulus sounds consist of simultaneously presented ascending and descending musical scales in such a way that the higher or lower tone at each instant is presented alternately to the right and left ear (See the score in Fig. 1a for C major scale as an example.). In the original scheme, Deutsch (1975) used pure tones of equal amplitude and 0.25 s in duration with no gaps between adjacent tones. Each phrase was presented repeatedly without intermission. Most right-handed listeners hear illusory percepts of smooth pitch contours from the higher half of the scale in the right ear and from the lower half in the left ear (Fig. 1b). Deutsch stated that the formation of scale illusion relies on the principle of grouping by frequency range, i.e., proximity of frequency, and that it markedly suppresses the perception of full scale tones actually present in the dichotic sequence. Behavioral and theoretical studies have revealed various aspects of scale illusion, such as the effects of handedness, ear advantage and grouping (Deutsch, 1975, 1985, 2013). However, the neural substrates underlying the formation of scale illusion remain mostly unknown.

In a previous study on scale illusion by magnetoencephalography (MEG), which has high temporal resolution, Kuriki et al. (2013a) measured short-term steady-state responses to amplitude-modulated tones at about 40 Hz using the tone sequence in Fig. 1a. They manipulated the sound level of the tones to increase monotonically as the frequency was decreased, so that the tone pitch that evoked the response could be inferred from the measured amplitude of the steady-state response. They observed the time course of the response that would be evoked by tones having a pitch contour fitting the percept of scale illusion. This illusion-contour response was statistically significant in participants who reported the illusion percept. In addition, this type of response was significant in the right hemisphere, but not in the left hemisphere. These results suggest that the neural activity that

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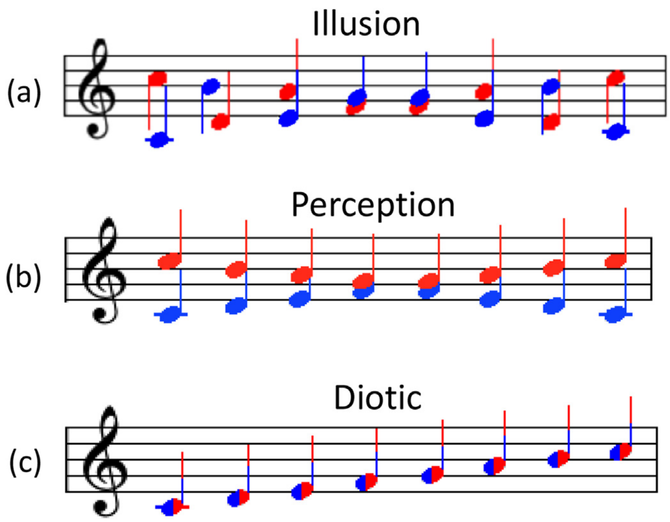

Fig. 1. Stimulus tones in a phrase used in the experiment. The tones presented in the left and right ears are shown in blue and red, respectively. (a) Illusion (ILL) stimulus that induced percepts of scale illusion, (b) perception (PCP) stimulus that followed pitch sequences of the percepts of scale illusion and (c) diotic (DIO) stimulus of ascending and descending (not shown in the figure) scale tones.

generated the illusion-contour response is closely related to the formation of scale illusion. Its anatomical location was estimated to be the primary auditory cortex (A1) and its neighbor, which corresponded to the generation site of the 40 Hz steady-state response (Engelien et al., 2000: Kuriki et al., 2013b; Pantev et al., 1996; Ross et al., 2005; Steinmann and Gutschalk, 2011). However, MEG has low sensitivity to deep sources, as well as to activities in higher/association cortices that generate responses not well time-locked to the sensory stimulus. Therefore, exploration of whole brain areas using versatile imaging techniques such as functional magnetic resonance imaging (fMRI) is needed.

In the present study, we carried out fMRI measurements to search for activation in the whole brain during the perception of scale illusion. For this, we measured BOLD activation while listeners binaurally perceived a sound stimulus that induced scale illusion (ILL stimulus; Fig. 1a). We also used a stimulus that mimicked the percepts of scale illusion (PCP stimulus; Fig. 1b) and a stimulus that consisted of diotic tones (DIO stimulus; Fig. 1c). The tones comprising the PCP sequence were common to those included in the ILL sequence as well as the DIO sequence. Assuming that the PCP stimulus was a good substitute for the percept of ILL stimulus, the activation difference of the ILL stimulus minus PCP stimulus would reflect the process to create a PCP-like percept from the ILL stimulus, i.e., the neural process forming the illusion, provided that acoustic effects are equivalent. We used the DIO stimulus to confirm relations of the BOLD activation of ILL > DIO and PCP > DIO expected from binaural suppression to DIO stimulus (Fujiki et al., 2002; Kaneko et al., 2003; Lazzouni et al., 2010), which originates in the auditory cortical interaction of identical tones given to the two ears. Since the binaural suppression is thought to be physiological and should be absent or very weak in response to the PCP and ILL stimuli, observation of ILL > DIO and PCP > DIO relations would assure that the activation of BOLD signal reflects the neural activities of the DIO/ILL/PCP stimuli.

The tone sequence of the ILL stimulus had discrete frequency jumps, while the sequence of the PCP stimulus was continuous without jumps following a smooth melody. That is, the frequency separation between adjacent tones was closer, on average, in the PCP sequence than in the ILL sequence. This may result in lower activation of the response to the PCP sequence than to the ILL sequence, confounding with the ILL formation process, if the adaptation effect is functioning. That is, an activation difference of ILL > PCP can be expected from both of adaptation and illusion formation processes. Adaptation has been observed in the auditory evoked potential as a reduction of response amplitude, which is larger when preceding tones have closer frequency separation (Näätänen et al., 1988; Nishimura et al., 2004). The strength of MEG response (N1m) to a succession of tones is lower for constant than for random frequency separation between the tones (Lagemann et al., 2012).

To discriminate whether the results can be explained by adaptation and/or illusion formation, we varied the delivery rate (tempo) of stimulus tones in separate fMRI sessions. Considering quantitative/qualitative data of adaptation and illusion available from previous studies, we adopted three different tempi. In terms of tone lengths (or intervals), they were 0.24 s, which followed the original study (Deutsch, 1975), 0.47 s, which was reported to induce stronger illusory percept in octave illusion than a length of 0.2 s tones (Brancucci et al., 2009), and 0.72 s, which corresponded to the tone length used in the MEG study (Kuriki et al., 2013a). Here, the octave illusion was originally shown by Deutsch 1974 using dichotic tone pairs that stand in octave relationship given to the two ears. With regard to how adaptation varies when tone interval is changed, the reduction of response to repeated tones was larger for shorter tone intervals (Budd et al., 1998; Lu et al., 1992; Rosburg et al., 2010). Similarly, the reduction for the second tone response in a two-tone sequence was larger for shorter onset-to-onset interval of the tones (Briley and Krumbholtz, 2013). No hemispheric difference was reported in the adaptation. Thus, we expected that the difference in activation between the ILL stimulus and PCP stimulus by adaptation would increase monotonically as the tempo of tones was raised, showing no significant difference in the two hemispheres. Alternatively, if the illusion formation process is dominant over the adaptation, ILL versus PCP activation should not be monotonic with the tempo change but would show a decrease as the tone length is shortened from 0.47 s to 0.24 s. Right hemisphere dominance of ILL versus PCP activation would be expected at the tone length of 0.72 s from the MEG study (Kuriki et al., 2013a) that revealed a significant illusion-related response in the right hemisphere, as described before.

We conducted region-of-interest (ROI) analysis for the ROI sites set in the superior temporal auditory cortex and examined how the magnitude of activation differed among the ILL/PCP/DIO stimuli and how their differences varied with the tempo. We also examined the activation of ILL − PCP contrast and inferred from the results, together with the results of the ROI analysis, the areas relevant to illusion formation and the functions executed in those areas. In the experiments, the occurrence of illusion by the ILL stimulus and the perception of as-presented PCP stimulus were confirmed by oral and written reports of the listeners. We found that the observed data of ILL versus PCP activation did not agree with the adaptation effects but were in line with the expectation of the illusion formation process. The results suggest that the right posterior area in the superior temporal region mostly contributes to the formation of scale illusion.

2. Materials and methods

2.1. Subjects and stimuli

Twenty-six healthy volunteers participated in the experiment. Data for 23 of the 26 participants, 20 males and 3 females with a mean (SD) age of 21.7 (1.9) years, were used for analysis; data for the other 3 participants were discarded because of excessive head