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Research paper

Independent or integrated processing of interaural time and level differences in human auditory cortex?

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ABSTRACT

Sound localization in the horizontal plane is mainly determined by interaural time differences (ITD) and interaural level differences (ILD). Both cues result in an estimate of sound source location and in many real-life situations these two cues are roughly congruent. When stimulating listeners with headphones it is possible to counterbalance the two cues, so called ITD/ILD trading. This phenomenon speaks for integrated ITD/ILD processing at the behavioral level. However, it is unclear at what stages of the auditory processing stream ITD and ILD cues are integrated to provide a unified percept of sound lateralization.

Therefore, we set out to test with human electroencephalography for integrated versus independent ITD/ILD processing at the level of preattentive cortical processing by measuring the mismatch negativity (MMN) to changes in sound lateralization. We presented a series of diotic standards (perceived at a midline position) that were interrupted by deviants that entailed either a change in a) ITD only, b) ILD only, c) congruent ITD and ILD, or d) counterbalanced ITD/ILD (ITD/ILD trading). The sound stimuli were either i) pure tones with a frequency of 500 Hz, or ii) amplitude modulated tones with a carrier frequency of 4000 Hz and a modulation frequency of 125 Hz.

We observed significant MMN for the ITD/ILD traded deviants in case of the 500 Hz pure tones, and for the 4000 Hz amplitude-modulated tone. This speaks for independent processing of ITD and ILD at the level of the MMN within auditory cortex. However, the combined ITD/ILD cues elicited smaller MMN than the sum of the MMN induced in response to ITD and ILD cues presented in isolation for 500 Hz, but not 4000 Hz, suggesting independent processing for the higher frequency only. Thus, the two markers for independent processing – additivity and cue-conflict – resulted in contradicting conclusions with a dissociation between the lower (500 Hz) and higher frequency (4000 Hz) bands.

1. Introduction

Sound localization in the horizontal plane is mediated by two primary cues: interaural time differences (ITD) and interaural level differences (ILD). The duplex-theory of sound localization states that these cues are processed separately (Strutt, 1907) and physiological studies have shown parallel binaural streams emerging from the superior olivary complex with ITD mainly processed within the medial and ILD within the lateral superior olive (for a review see Grothe et al., 2010). In free-field conditions, ITD and ILD will usually induce congruent location estimates, however, in a reverberant environment the relationship between the two cues can change: as ITD and ILD cues are differently affected by reverberation (Ihlefeld and Shinn-Cunningham, 2011; Rakerd and Hartmann, 2010), we need to have flexibility in the weighting of ITD and ILD in different every-day environments to preserve accurate sound localization. Furthermore, the relationship of the two cues is necessarily subject to plastic changes: when our body and our head

Abbreviations: EEG, electroencephalography; ILD, interaural level difference; ITD, interaural time difference; LSO, lateral superior olive; MEG, magnetoencephalography; MMN, mismatch negativity; MSO, medial superior olive; SL, sensation level; 2AFC, two-alternative-forced-choice

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grows in size during childhood, the weighting of ITD and ILD cues requires recalibration (see King et al., 2001), and in late adult life when our hearing capabilities decline such a recalibration is possibly needed again.

Now, the question arises at what stage of the auditory pathway ITD and ILD cues are processed in an integrated manner. A previous electroencephalography (EEG) study has shown independent processing of ITD and ILD up to the level of the auditory cortex, employing mismatch negativity (MMN) as a measure (Schröger, 1996). In particular, that study found that a combined change of ITD and ILD leads to a MMN response comparable to the sum of MMN responses to single deviants (ITD or ILD). Thus, Schröger (1996) has provided evidence for additivity of ITD and ILD, suggesting independent processing. An alternative approach to study independence versus integration is to devise stimuli containing cues that counterbalance each other: so-called ITD/ILD cue trading (e.g., Shaxby and Gage, 1932; Hafter and Jeffress, 1968; Stecker, 2010). In a recent psychophysical study, Furukawa (2008) regarded hypothetical ITD and ILD processors as "channels", each of which has its own noise source. The noises in the two channels should be uncorrelated if the channels are independent. A perfect correlation of the noises would indicate that the ITD and ILD information is integrated and processed in a common channel. Furukawa (2008) evaluated the degree of independence of the two channels by estimating the correlation coefficient of the noises on the basis of signal detection theory (Green and Swets, 1974). The results indicated that the ITD and ILD channels are not completely independent and that the degree of independence is higher for low (125 and 500 Hz) than for high-frequency stimuli (4 kHz). The results of Schröger (1996) also hint at a difference between frequency bands, in his case between a 900 Hz pure tone and a complex tone, containing a 600 Hz and a 3000 Hz sub-component.

The current study aimed at providing evidence for either independent or integrated processing of ITD and ILD at the level of the MMN in auditory cortex by stimulating with ITD/ILD in isolation, ITD/ILD combined congruently or ITD/ILD combined incongruently (trading stimulus). Furthermore, given the results of Furukawa (2008) suggesting different mechanisms of cue integration for different frequency bands, we stimulated with sounds at two different frequency ranges: a 500 Hz pure tone and a 4000 Hz tone with 125 Hz amplitude modulation. We hypothesized that completely independent processing should lead to similar MMN for the sum of the isolated cues and the congruent and incongruent cues. This would suggest additivity and invariance of the MMN to the sign of the lateralization cue. In contrast, integrated processing would be suggested by a difference between the sum of the isolated cues and the combined congruent cues (non-additivity) and by larger MMN for the congruent versus the incongruent cues. As we will describe in the following, our results did not fit entirely into either category, but revealed conflicting results for the two measures of independence, additivity and cue-conflict.

2. Material and methods

2.1. Subjects

We conducted the experiments on twenty healthy, normal hearing subjects. One subject was excluded due to an inability to achieve ITD/ILD cue trading in one of the conditions. The remaining sample consisted of 12 male and 7 female subjects with an average age of 26.1 years (range: 20–37) and all subjects were right-handed (one subject was originally left-handed but switched to right-handedness in childhood). All subjects were informed of the aims and risks of the experiment and gave written informed consent. The experiments were performed in accordance with the ethical standards laid down in the declaration of Helsinki of 1964 and the guidelines approved by the local ethics committee of the Graduate School of Medicine and Faculty of Medicine, Kyoto University.

2.2. Experimental stimuli and apparatus

The sound stimuli (sampling rate: 44.1 kHz) were either pure tones with a carrier frequency of 500 Hz (PT500) or amplitude-modulated tones with a carrier frequency of 4 kHz, amplitude-modulated by a half-wave rectified 125 Hz sinusoid (AM4000). The latter constituted a so-called "transposed stimuli" (van de Par and Kohlrausch, 1997; Bernstein, 2001), which has been used in previous psychophysical studies of ITD/ILD cue trading (Furukawa, 2008). Similar to previous studies employing transposed tones (Bernstein and Trahiotis, 2002; Furukawa, 2008), the modulator was low-pass filtered with a cutoff frequency of 2 kHz to restrict the energy of the resulting stimulus to the ± 2 kHz range around the carrier frequency, but unlike these studies, no low-pass filtered Gaussian noise was added to mask low-frequency distortion products. All sound stimuli had a duration of 100 ms and were shaped by a 50 ms rising and falling diotic cosine ramp. Sound pressure was adjusted to 45 dB above individual sensation level (SL) for the two types of sounds separately. Simulated in-head lateralization was induced by adding either ITD or ILD. The ILD was implemented by increasing the level in one ear and decreasing it in the other relative to the center level (45 dB SL), so that the average for the two ears on a decibel scale was the center level. Five types of stimuli were created for each tone frequency (see Fig. 1): a) stimuli without ITD or ILD: <0>, b) stimuli with negative/positive ITD and no ILD to elicit the perception of a left/right-lateralized sound: <ITD>, c) stimuli with negative/positive ILD and no ITD to elicit the perception of a left/right-lateralized sound: <ILD>, d) stimuli with negative/positive ILD and congruent ITD to elicit the perception of a further left/right-lateralized sound (e.g., Domnitz and Colburn, 1977; Whitworth and Jeffress, 1961): <ITD + ILD>, and e) stimuli with negative/positive ILD and incongruent positive/negative ITD to elicit the perception of a central sound source: <ITD-ILD>. For PT500, the ITD was always -200 or $+200$ μs and the ITD for the AM4000 was determined by matching the perceived lateralization of the AM4000 to that of the PT500. This matching led on average to ITDs of -587 ± 316 (SD) and $+448 \pm 210$ (SD) μs. The ILDs were determined by a psychophysical ITD/ILD cue trading procedure.

Sounds were delivered via Etymotic Research ER4 in-ear-headphones (Etymotic Research Inc., Elk Grove Village, IL, USA). Stimulus presentation was controlled by a PC using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007), running in a Matlab environment (The Mathworks Inc., Natick, MA, USA). During all parts of the experiment, subjects were seated in a single-walled acoustic booth (AT-66, RION Co., Ltd., Kokubunji, Japan).

2.3. Procedure

Before the main EEG experiment, several psychophysical tests were conducted to determine the stimulus parameters individually. First, we measured the diotic sensation levels for each stimulus type (PT500, AM4000) separately, employing an adaptive sound detection task. In more detail, the 50% sensation threshold was determined with a weighted up-down method (Kaernbach, 1991). Step-size started with 16 dB and was then halved at each reversal, until it reached 1 dB after which it remained constant for six further reversals. The sensation threshold was determined as the median of these last six reversals. Second, to ensure a similar extent of lateralization for the PT500 and AM4000 stimuli, we instructed