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Division of labor between left and right human auditory cortices during the processing of intensity and duration

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ABSTRACT

Intensity and duration are important parameters for the processing of speech and music. Neuroimaging results on the processing of these parameters in tasks involving the discrimination of stimuli based on these parameters are controversial. Depending on the experimental approach, varying hypotheses on the involvement of the left and right auditory cortices (ACs) have been put forward. The aim of the present functional magnetic resonance imaging (fMRI) study was to find differences and commonalities in location and strength of brain activity during the processing of intensity and duration when the same stimuli have to be actively categorized according to these two parameters. For this we used a recently introduced method to determine lateralized processing in the AC with contralateral noise. Harmonic frequency modulated (FM) tone complexes were presented monaurally without and with contralateral noise. During categorization of the tones according to their intensity, contralateral noise increased activity mainly in the left AC, suggesting a special role for the left AC in this task. During categorization of tones according to their duration, contralateral noise increased activity in both the left and the right AC. This suggests that active categorization of FM tones according to their duration does not involve only the left AC as has been suggested, but also the right AC to a substantial degree. The area around Heschl's sulcus seems to be the most strongly involved during both intensity and duration categorization, albeit with different lateralization. Altogether the results of the present study support the view that the lateralized processing of the same stimuli in the human AC is strongly modulated by the given task (top-down effect).

Introduction

For the perception of complex auditory stimuli like speech and music, the processing of different acoustic properties such as frequency, intensity, and duration is important. Although different hypotheses about lateralized processing in the auditory cortex (AC) exist, it is still an unsolved issue. One hypothesis by Zatorre et al. (2002) suggests that the left AC has a better temporal resolution and the right AC has a better spectral resolution. According to the asymmetric sampling in time (AST) hypothesis by Poeppel (2003), the right AC preferentially extracts information from long integration windows (150–250 ms) and the left AC preferentially extracts information from short integration windows (<40 ms). In addition, it has been demonstrated that listening to sounds elicits activity in the brain that strongly depends on the listening strategy (top-down effect) (Bradshaw and Nettleton, 1981; Brechmann and Scheich, 2005; Brechmann et al., 2007; Scheich et al., 2007; Zatorre and Gandour, 2008). The aim of the present fMRI study was to find differences and commonalities in location and strength of activity during the processing of intensity and duration when the same stimuli have to be actively categorized according to these two parameters.

Although the effect of an increase in intensity of auditory stimuli on the amount of neuronal activity is well investigated, neuroimaging studies using intensity as a task-relevant stimulus feature are rare. Belin et al. (1998) suggested that two networks are involved in the discrimination of intensity, i.e., a right frontoparietal network for attentional processing and a region in the right posterior temporal gyrus for sensory computation of differences in sound intensity. Results of a psychoacoustic study also point to stronger involvement of the right hemisphere in the discrimination of intensity (Brancucci et al., 2005). In agreement with these results, the number of errors during loudness discrimination increases after right but not after left temporal lobectomy (Milner, 1962). In contrast, an fMRI study (Reiterer et al., 2008) showed a leftward dominance of activity in the temporal cortex including AC during an intensity discrimination task. Another psychoacoustic study investigating loudness discrimination did not reveal differences between left and right ear presentations (Dykstra et al., 2012). In all of the previous studies but one (Belin et al., 1998),

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the participants had to compare the intensity of two tones. Neither of the previous studies on intensity discrimination used a categorization task or FM tones as we have done in the present study. Therefore, the controversial results on intensity discrimination do not allow the formulation of a clear hypothesis as to whether the active categorization of FM tones according to intensity involves more the left or the right AC, or both ACs equally.

Results on the lateralized processing of duration are also controversial. Belin et al. (2002) suggest that two networks are involved in the discrimination of duration: a right fronto-parietal network, which they suggest is involved in the allocation of sensory attentional resources, and a network of right prefrontal cortex, basal ganglia, and cerebellum, responsible for the temporal aspects of the task. They did not find any involvement of the temporal lobe. In contrast, an fMRI study using FM tones suggests a stronger involvement of the left AC in the discrimination of duration (Brechmann and Scheich, 2005). This was confirmed by a learning study, also involving short and long FM tones (Puschmann et al., in press). Another fMRI study also showed a left lateralization of activity in the temporal lobe during duration discrimination but increasing activity in the right temporal cortex with increasing accuracy of discrimination (Reiterer et al., 2005). Results of psychoacoustic studies suggest either a stronger involvement of the left hemisphere in the discrimination of duration (Brancucci et al., 2008; Mills and Rollman, 1979) or a stronger involvement of the right hemisphere (Buchtel et al., 1978). For the present study, we hypothesized that we would find a stronger involvement of the left AC in the categorization of FM tones according to their duration. We based this hypothesis on the findings by Brechmann and Scheich (2005) and Puschmann et al. (in press) because they also used FM tones in combination with a categorization task, in contrast to the other studies.

In the present study, we used a method that can reveal lateralized processing in the AC by presenting the task-relevant stimuli monaurally, with or without additional noise to the contralateral ear (Behne et al., 2005, 2006). This method makes use of the contralaterality of the auditory pathway where in the AC information from the contralateral ear dominates and input from the ipsilateral ear is suppressed (Brancucci et al., 2004; Kaneko et al., 2003; Kimura, 1967). The method probes the contribution of the left and right ACs independently by determining the fMRI activity elicited by task-relevant stimuli presented ipsilaterally without or with contralateral noise. Any significant increase of activity by contralateral noise indicates a significant contribution of the hemisphere to solving the task. Thus, the method is able to determine hemispheric lateralization if the additional noise only impacts on the activity of one hemisphere. We proposed that the processing of task-relevant stimuli that are presented to the ipsilateral ear has to take place under reduced signal-to-noise ratio (SNR) conditions due to the presentation of additional noise to the contralateral ear. We hypothesize that the increase in activity results from mechanisms that are necessary to compensate for the reduced SNR to still adequately solve the task. Such an effect can be revealed by comparing the activity elicited in the conditions without noise and the respective condition with noise. A major advantage of this method is that only one task on the identical set of stimuli is sufficient to make a statement about lateralized processing in the AC. This was confirmed with this method for two functions known to be strongly lateralized, i.e., the processing of speech material where noise increased activity mainly in the left AC (Behne et al., 2006; Stefanatos et al., 2008), and the categorization of the direction of frequency modulation where noise increased activity only in the right AC (Behne et al., 2005).

The present study examines the active categorization of the two parameters intensity and duration employing identical sets of stimuli in a within-subject design. The aim was to directly test the differential contribution of the left and right auditory cortices during the processing of these basic parameters for auditory perception.

Materials and methods

Participants

Sixteen right-handed volunteers (Edinburgh Handedness Inventory; laterality quotient $\geq +73$) with normal hearing (hearing level $\leq$ 20 dB from 125 Hz to 8 kHz, interaural difference at each tested frequency $\leq$ 10 dB) participated in the study. Participants (age 20–36 years, mean age 28 years, 7 females) gave written informed consent to the study, which was approved by the ethics committee of the University of Magdeburg. Five additional participants were excluded from the final analysis because their hit rate was below 70% for one stimulus category (3 cases) or because of technical problems (2 cases).

Stimuli and tasks

Harmonic, linearly FM tone complexes served as acoustic stimuli. They lasted 400 or 600 ms including a linear rise/fall time of 10 ms. Each tone complex consisted of five harmonics of decreasing amplitude (100% amplitude for fundamental frequency, 80% for 2nd harmonic, 60% for 3rd, 40% for 4th, 20% for 5th). The center frequencies (f_C) of the fundamentals were 140 Hz, 180 Hz, 220 Hz … 820 Hz. The starting and end frequencies were calculated by f_C (Hz) $\pm$ f_C (Hz) $*$ 0.5 $*$ duration of the tone (s). Two sets of FM stimuli were used: a soft and a loud set which differed in amplitude by 7 dB. The 7 dB difference between the two sets of stimuli was defined in prior tests in order to achieve a similar performance for both tasks. The different perception of intensity level due to different frequencies was reduced by decreasing the amplitude of the higher tones in steps of 0.25 dB for each two f_C steps used. Therefore, the mean amplitude (root mean square) of the FM tone complex with the highest frequencies was 2 dB softer than the amplitude of the FM tone complex with the lowest frequencies. Nevertheless, due to the different f_C and the FM the perceived intensity of the FM tones within the two (soft and loud) sets varied. During the single session, the FM tones were presented in 30 stimulation blocks of 30 s each, which alternated with 31 blocks of 20 s silence. Within each block of stimulation, 24 tones were presented with 750 ms of silence between the tones. Each stimulation block included 12 short tones and 12 long tones, 12 soft tones and 12 loud tones, 12 upward FMs and 12 downward FMs. The tones within a block were presented either binaurally, monaurally to the left ear without noise, monaurally to the right ear without noise, monaurally to the left ear with continuous white noise to the right ear or monaurally to the right ear with continuous white noise to the left ear. The amplitude (root mean square) of the noise was 2 dB higher than the mean amplitude of all tones. The amplitude of the binaurally presented FM tones was 4 dB lower than the amplitude of the monaurally presented tones in order to achieve a similar intensity percept. Six blocks for each of the five conditions were presented in pseudo-randomized order such that two consecutive blocks did not belong to the same condition.

The same stimuli were presented first in one psychoacoustic session and then on two other days in two fMRI sessions. The psychoacoustic session was done to evaluate if the subjects were able to perform the task and to minimize learning effects in the initial phase of the fMRI sessions. The participants had to solve two different tasks: one task per day during fMRI and both tasks at one day in the psychoacoustic session. They had to categorize the tones (1) according to their duration (short vs. long) or (2) according to their intensity (soft vs. loud). The order of both tasks was balanced across participants. The participants had to press a button with their right index finger for one category of stimuli and another button with their right middle finger for the other category. The stimuli/hand-to-button assignment was balanced across the group.