NeuroImage 79 (2013) 371–382

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Tactile stimulation and hemispheric asymmetries modulate auditory perception and neural responses in primary auditory cortex

M. Hoefer [a,b,*], S. Tyll [a,b], M. Kanowski [b], M. Brosch [c], M.A. Schoenfeld [b,c], H.-J. Heinze [b,d], T. Noesselt [a,d]

[a] *Department of Biological Psychology, Otto-von-Guericke-University Magdeburg, Postfach 4120, 39106 Magdeburg, Germany*
[b] *Department of Neurology, Otto-von-Guericke-University Magdeburg, Leipziger Str. 44, 39120 Magdeburg, Germany*
[c] *Leibniz Institute of Neurobiology, Brenneckestraße 6, 39118 Magdeburg, Germany*
[d] *Center for Behavioral Brain Sciences, Magdeburg, Germany*

ARTICLE INFO

Article history:
Accepted 27 April 2013
Available online 9 May 2013

Keywords:
Audiotactile
Human
fMRI
Multisensory
Temporal integration

ABSTRACT

Although multisensory integration has been an important area of recent research, most studies focused on audiovisual integration. Importantly, however, the combination of audition and touch can guide our behavior as effectively which we studied here using psychophysics and functional magnetic resonance imaging (fMRI). We tested whether task-irrelevant tactile stimuli would enhance auditory detection, and whether hemispheric asymmetries would modulate these audiotactile benefits using lateralized sounds. Spatially aligned task-irrelevant tactile stimuli could occur either synchronously or asynchronously with the sounds. Auditory detection was enhanced by non-informative synchronous and asynchronous tactile stimuli, if presented on the left side. Elevated fMRI-signals to left-sided synchronous bimodal stimulation were found in primary auditory cortex (A1). Adjacent regions (planum temporale, PT) expressed enhanced BOLD-responses for synchronous and asynchronous left-sided bimodal conditions. Additional connectivity analyses seeded in right-hemispheric A1 and PT for both bimodal conditions showed enhanced connectivity with right-hemispheric thalamic, somatosensory and multisensory areas that scaled with subjects' performance. Our results indicate that functional asymmetries interact with audiotactile interplay which can be observed for left-lateralized stimulation in the right hemisphere. There, audiotactile interplay recruits a functional network of unisensory cortices, and the strength of these functional network connections is directly related to subjects' perceptual sensitivity.

Introduction

During the last decade scientific interest in multisensory interplay (MSI) and its neural foundation has increased remarkably (see Driver and Noesselt, 2008, for review). At first, higher-order association cortex and subcortical areas like the superior colliculi were perceived as key regions in which MSI might take place (Lewis and Van Essen, 2000; Meredith and Stein, 1986; Wallace et al., 1993). However, this view has been challenged by more recent studies indicating that MSI also takes place in low-level sensory-specific areas (for review see e.g. Cappe et al. (2009b)) and can even occur at subcortical stages (Cappe et al., 2009a; Musacchia et al., 2006; Noesselt et al., 2010).

So far, most human imaging studies on MSI focused on audiovisual and visuotactile pairings (e.g. Kim and James, 2010; Macaluso et al., 2000; Molholm et al., 2002; Ramos-Estebanez et al., 2007; Shams et al., 2002; Werner and Noppeney, 2010a). Relatively few imaging studies have used audio–tactile combinations (Foxe et al., 2002; Schürmann et al., 2006; for electrophysiological effects see e.g. Caetano and Jousmäki, 2006; Foxe et al., 2000; Gobbelé et al., 2003; Murray et al., 2005), though auditory and tactile signal transduction times from the ear and skin are much faster than visual signal transduction times. Therefore, audiotactile integration may rely on a mechanism, which is distinct from those of audiovisual and visuotactile interplay. In accord, early modulations in macaques' primary auditory cortex have been found for tactile but not visual stimulation (Lakatos et al., 2007). Thus, we chose to identify the neural basis of audiotactile interplay in humans and specifically focused here on auditory detection performance.

Previous electrophysiological studies in macaques reported tactile influences on low-level auditory cortex (e.g. Lakatos et al., 2007; for review see Kayser and Logothetis, 2007). Further, according to tracing studies in macaques, several sources of somatosensory inputs to auditory cortex exist, including insular (Hackett et al., 2007), somatosensory (Cappe and Barone, 2005) and multisensory cortex plus posterior thalamic nuclei (De la Mothe et al., 2006; for review see Musacchia and Schroeder, 2009; Smiley and Falchier, 2009). However, none of these studies has directly linked their neurophysiological/anatomical markers with behavior.

Like in many cortical functions, hemispheric asymmetries may also play a role in MSI: it seems to predominantly recruit right-hemispheric

---

* Corresponding author at: Otto-von-Guericke-University Magdeburg, Department of Biological Psychology, Postfach 4120, 39106 Magdeburg, Germany. Fax: +49 391 6711947.
E-mail address: maria.hoefer@med.ovgu.de (M. Hoefer).

1053-8119/$ – see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.neuroimage.2013.04.119

cortex (e.g. Downar et al., 2000; Giard and Peronnet, 1999; Molholm et al., 2002) though others have found less lateralized responses and evidence for integration in the left hemisphere (e.g. Kayser et al., 2005; Murray et al., 2005; see Ramos-Estebanez et al., 2007 for left-hemispheric effects in visuotactile interplay). In line with the notion of right-hemispheric dominance, Bushara et al. (2001) found a right-sided network of regions for audiovisual temporal judgments; and Noppeney and colleagues reported correlations of strength of fMRI-signals in the right STS, auditory cortex and MT+ with behavioral responses using audiovisual stimuli (Lewis and Noppeney, 2010; Werner and Noppeney, 2010a). This indicates that in a multisensory context neural responses in the right hemisphere may be more closely linked to behavioral effects. However, none of the studies above directly tested for a hemispheric specialization with lateralized stimuli.

On the behavioral level several effects for audio–tactile stimulus combinations have been reported: For instance, the ventriloquist illusion reportedly also works for audio–tactile pairings (Bruns and Röder, 2010). Moreover, task-irrelevant tactile stimuli may also improve auditory sensitivity (Gillmeister and Eimer, 2007), though effects of hemispheric asymmetries were not tested there.

In a first human psychophysical experiment we directly tested for an increase in auditory sensitivity due to touch and for an effect of hemispheric dominance using left and right-sided stimulation outside the MR-scanner. We then investigated in an fMRI-experiment how any increase in auditory sensitivity by a co-occurring touch and any effects of stimulated side relate to the modulation of regional fMRI-signals, their inter-regional effective connectivity, and how these changes in connectivity scale with subject-specific behavioral performance.

Materials and methods

Participants

All subjects were paid volunteers (6 €/h) and naïve with respect to the purpose of the study (except for one subject which is an author). They provided informed consent in accord with local ethics clearance and had normal hearing and normal or corrected-to-normal vision. Recent studies also indicate that musical experience can shape multisensory integration (see e.g. Paraskevopoulos et al., 2012a, 2012b). However, this influence was less known when we started our experiment, thus was not acquired.

Behavioral experiment outside the scanner

This audiotactile experiment was run outside the scanner to confirm that any behavioral effects could not be attributed to the scanner environment. 24 subjects (eleven female; age range: 19–30 years, one left-handed) participated. Two subjects (one female) were excluded due to performance below chance level in the auditory detection trials. Thus, the data of 22 subjects were analyzed.

fMRI experiment

23 subjects (eleven female; age range: 21–31 years, two left-handed) participated in an fMRI experiment, to identify the neural underpinnings of the behavioral effects. Two subjects (both female) were excluded from the fMRI analysis because they stopped the experiment prior to the completion of all 6 experimental sessions; a third subject (male) was excluded because his movement parameters exceeded 5 mm in abrupt head movements. We included the behavioral data of all subjects in the later behavioral analysis, not to unduly bias the behavioral results; for fMRI-analysis the data of 20 subjects were used.

Stimuli and apparatus

The following stimulus conditions were employed (see Fig. 1a): (a) unisensory: auditory stimulation (A), tactile stimulation (T), and (b) multisensory: synchronous audio–tactile stimulation (AT_S) and asynchronous audio–tactile stimulation with auditory stimulation *preceding* the tactile stimulus by 200 ms (AT_{AS}). Further, there was a baseline condition in which no stimulus was presented (N). Auditory stimuli were presented on the left or right side (behavior: 11° visual angle; fMRI: 10° visual angle). Note that the lateralized auditory stimulation used here was similar to those used in earlier auditory studies, which yielded to approximately 80% correct responses in an auditory localization task (see Bonath et al., 2007). Left- and right-sided presentations were counterbalanced and tactile stimulation was equally likely for target and non-target trials. This design led to ten experimental conditions (synchronous bimodal stimulation, asynchronous bimodal stimulation, unimodal tactile stimulation, and unimodal auditory stimulation, plus the baseline condition each for the left and the right side). Albeit the two baseline conditions are virtually identical we treated them as two separate conditions since they were intended as control condition for each side. Due to a suggestion by an anonymous reviewer we have additionally calculated the behavioral data with a collapsed baseline condition (see Supplementary Tables S1, S4 and S5), which gave virtually identical results.

Note that bimodal conditions were always presented on the same side. This was realized by attaching two piezo-electric speakers to the left and the right side of the central fixation point at the top of the scanner bore. Thus, a free-field auditory stimulation was used, instead of monaural stimulation with headphones (Jäncke et al., 2002; Scheffler et al., 1998). Monaural stimulation may have yielded a different activation pattern, but was not used in order to maximize audiotactile spatial congruence which is essential for multisensory integration to occur (e.g. Stein and Stanford, 2008). Thus, we chose free-field stimulation because of its high ecological validity.

The irrelevant tactile stimuli were non-vibratory pressure pulses. They were delivered via diaphragms inflated by pulses of pressured air, controlled by a somatosensory stimulus generator (4-D Neuroimaging, San Diego, California). Two lip clips were applied to the lower lip (left and right corner of the mouth). The pneumatic bursts caused a 50 ms lasting deflection of the membrane of the lip clips, which felt like a soft touch to the lip (see below for pressures employed in the two experiments). We chose the lips instead of fingertips for stimulation, because they are very sensitive, have a robust contralateral cortical representation (see e.g. Iannetti et al., 2003; Nguyen et al., 2004; Penfield and Boldrey, 1937), and because they are located close to the auditory stimulation which was close to the head. Hence, we minimized audiotactile spatial disparity in our experiments.

Behavior outside scanner

Visual stimuli were presented on a 21 inch CRT monitor (Samsung SyncMaster 1100MB). Central fixation was presented throughout the experiment and subjects were instructed to fixate. Auditory stimuli were presented via two piezo-electric speakers (to mimic stimulus presentation inside the scanner) attached to the left and right side of the monitor (11°/visual angle). Each auditory target stimulus was a white noise sound burst with a duration of 50 ms (35 dB on average).

fMRI

Stimulation inside the scanner was identical to outside stimulation with the following exceptions: visual response cues were presented via a mirror-system onto a rear-projection screen located at the base of the scanner bed. Auditory stimuli were presented via two piezo-electric speakers attached to the top of the scanner bore (+/−10°/visual angle). All stimuli were presented during silent periods (2 s) interleaved with periods of scanning (2 s) to prevent scanner noise from interfering with the perception of the auditory and tactile stimuli (rapid–sparse sampling protocol, see below for scanning protocol).