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Neural basis of multisensory looming signals

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ABSTRACT

Approaching or looming signals are often related to extremely relevant environmental events (e.g. threats or collisions) making these signals critical for survival. However, the neural network underlying multisensory looming processing is not yet fully understood. Using functional magnetic resonance imaging (fMRI) we identified the neural correlates of audiovisual looming processing in humans: audiovisual looming (vs. receding) signals enhance fMRI-responses in low-level visual and auditory areas plus multisensory cortex (superior temporal sulcus; plus parietal and frontal structures). When characterizing the fMRI-response profiles for multisensory looming stimuli, we found significant enhancements relative to the mean and maximum of unisensory responses in looming-sensitive visual and auditory cortex plus STS. Superadditive enhancements were observed in visual cortex. Subject-specific region-of-interest analyses further revealed superadditive response profiles within all sensory-specific looming-sensitive structures plus bilateral STS for audiovisual looming vs. summed unisensory looming conditions. Finally, we observed enhanced connectivity of bilateral STS with low-level visual areas in the context of looming processing. This enhanced coupling of STS with unisensory regions might potentially serve to enhance the salience of unisensory stimulus features and is accompanied by superadditive fMRI-responses. We suggest that this preference in neural signaling for looming stimuli effectively informs animals to avoid potential threats or collisions.

Introduction

The ability to discriminate between approaching (looming) or receding events is critical for survival in the environment. From an evolutionary perspective it seems to be highly advantageous for animals (including humans) to differentiate between suddenly approaching potential threats and spatially disengaging harmless events. A successful detection of potential threats gives the organism time to prepare a defense or motor response (Bach et al., 2009; Grassi, 2010) and thus increases the likelihood of survival. Even today's humans, as members of the common road traffic, are exposed to potential threats of suddenly approaching objects, to which they should react immediately (Wann et al., 2011).

Concordant with these theoretical considerations, several behavioral studies reported that the perception of auditory and visual looming and receding signals differs despite identical overall stimulus energy (auditory modality: Gray, 2011; Hall and Moore, 2003; Maier and Ghazanfar, 2007; Schlauch et al., 2001; visual modality: Franconeri and Simons, 2003; Schiff et al., 1962; Takeuchi, 1997). The only discrepancy between those signals is their temporal profile: looming signals increase in amplitude or size over time whereas for receding signals the temporal pattern is reversed. Thus, these particular looming stimulus dynamics seem to selectively enhance perceptual sensitivity and/or a cognitive bias in comparison to receding signals if presented unimodally (Ghazanfar et al., 2002; Parker and Alais, 2007). In accord, neural processing of looming stimuli is related with enhanced single cell firing (Liu et al., 2011; Maier and Ghazanfar, 2007; Peron and Gabbiani, 2009) and increased fMRI-signals in cortical regions (Seifritz et al., 2002; Wittmann et al., 2010).

However, most everyday events provide information that is picked up by more than one sense; e.g. for the perception of road traffic we rely on both visual and auditory cues and combine them into a unified multimodal percept (Alais et al., 2010; Driver and Noesselt, 2008; Ghazanfar and Schroeder, 2006; Stein and Stanford, 2008). In the case of multisensory looming signals several behavioral studies reported a behavioral benefit over receding signals, supplementing the results of unimodal stimulation. Preferential looking tests demonstrated that monkeys (Maier et al., 2004) and young infants (Lewkowicz, 2008;

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Walker-Andrews and Lennon, 1985) are able to discern between multisensory looming and receding signals, thereby pointing to a potential phylogenetic basis for this effect. Moreover, auditory looming signals have been related to a behavioral benefit in visual orientation sensitivity in humans (compared to receding or static signals, Leo et al., 2011). Finally, Cappe et al. (2009) reported a selective integration effect for multisensory looming signals in humans with speeded reaction times, enhanced target detection and increased subjective ratings of movement. Notably, significantly enhanced detection rates were also found for multisensory looming stimuli compared to static multisensory stimuli in that study. Together, these results suggest a selective behavioral gain for multisensory looming signals in humans.

The neuroanatomical and neurophysiological basis of this multisensory looming effect is not yet fully understood in mammals. To our knowledge, only three studies examined the neural underpinnings of audio-visual looming processing so far (Cappe et al., 2012; Maier et al., 2008; Romei et al., 2009). However, they only investigated the effects in macaque A1 and STS with intracranial recordings (Maier et al., 2008), or they studied the effect by means of TMS-induced phosphenes in humans (Romei et al., 2009), or they investigated the temporal dynamics of this effect using event-related potentials (ERPs, Cappe et al., 2012) which lack the spatial resolution for a precise identification of the neural underpinnings. Thus, the exact network of brain regions related to multisensory looming processing has yet to be discovered. In the present study we set out to identify the neural basis of audiovisual looming signals in the human brain using event-related functional magnetic resonance imaging (fMRI).

In addition, we sought to further characterize the underlying neurophysiological response profile within looming-sensitive brain areas by comparing uni- with multisensory looming and receding stimuli, because the exact shape of multisensory response profiles is still a matter of an ongoing debate (e.g. Cappe et al., 2010): previous single cell studies have reported that the integration of different modalities can lead to a non-linear modulation of neural activity in response to multisensory stimulation relative to the summed unisensory responses (e.g. Stein and Meredith, 1993). However, for population responses (as measured with fMRI) nonlinear response enhancement with multisensory responses exceeding the sum of the unisensory responses have not always been observed (Beauchamp, 2005b), and some authors suggested that superadditive responses might only be found with near-threshold stimulation (e.g. Stevenson et al., 2007). Therefore, several alternative analysis approaches for identifying multisensory integration have been proposed. These include the comparison of multisensory responses to the mean of (mean criterion), or the maximum of (max criterion) unisensory responses (Beauchamp, 2005b; Calvert et al., 2001; Love et al., 2011) instead of summed unisensory responses (super-additive criterion). Here, we directly compared all three criteria for classification of multisensory response profiles in response to audio-visual looming stimuli. In addition to the whole brain voxel-wise group-analysis we complemented our analysis by a subject-specific regions of interest analysis (ROIs) within unisensory and putatively multisensory brain regions, because some previous studies suggested that voxel-wise group-analyses may be relatively insensitive for classification of particular response profiles, especially super-additive effects (Beauchamp, 2005b; Stevenson and James, 2009).

Finally and in addition to the identification of looming-sensitive regions and characterization of intraregional response profiles we also tested for the functional network selectively engaged in the processing of audiovisual looming stimuli.

Materials and methods

Participants

Twenty-one (8 female, aged 19–33, mean: 23.9 years, SD: 3.87) right-handed, subjects participated in the fMRI study. Participants were healthy, had no preexisting neurological or psychiatric disorders, reported normal hearing and normal or corrected-to-normal vision and were paid for participation. The study was approved by local ethics, and the subjects gave written informed consent. Three subjects were excluded from analysis due to scanner malfunctioning or large head movements (exceeding 1° and/or 5 mm in abrupt movements in more than half of the runs).

Stimuli and procedure

Auditory stimuli consisted of a 3 kHz sinus tone with a rising (looming, 35 dB to 90 dB SPL, abbreviation: AL) or falling (receding, 90 dB to 35 dB SPL, abbreviation: AR) amplitude to generate the perception of movement (see Fig. 1 top; Audacity was used for stimulus generation; http://audacity.sourceforge.net/). Tones (duration: 500 ms with 10 ms on/offset ramps to avoid clicks) were presented via piezo-electric speakers attached to the top of the scanner bore to maximize audiovisual alignment. Visual stimuli consisted of centrally presented black disks, which expanded (looming, abbreviation: VL) or contracted (receding, abbreviation: VR) on a white background over a period of 500 ms (range: 1.2°–12.8°, see Fig. 1 top). Stimuli were either presented unimodally or audiovisually (Presentation 9.13—Neurobehavioral Systems) resulting in eight stimulus conditions (2 visual, 2 auditory and 4 audiovisual). Other behavioral studies used also a static sound condition (see e.g. Cappe et al., 2009). However, for fMRI-research it is essential to keep the stimulation across conditions as similar as possible. Therefore we chose to only use looming and

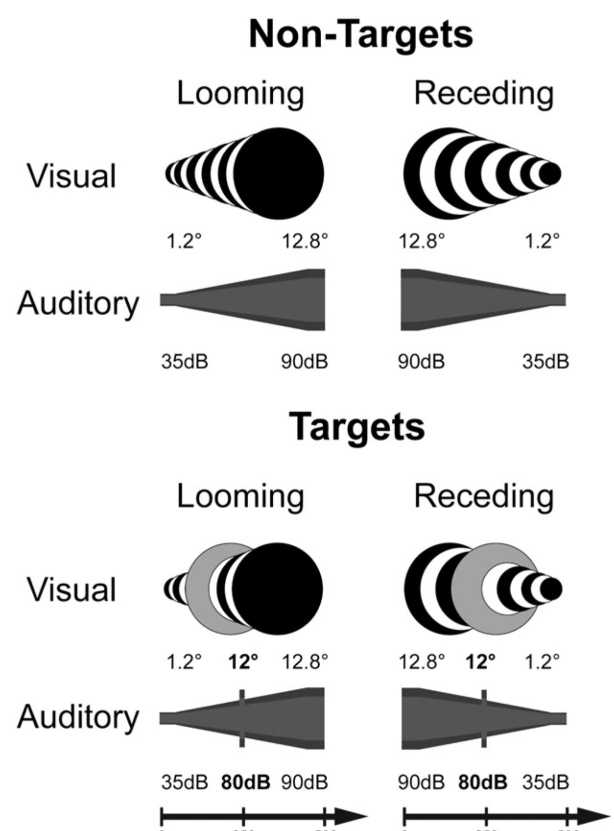

Fig. 1. Experimental design. Top: schematic illustration of visual and auditory stimuli, shown for looming and receding conditions. During the multisensory conditions visual and auditory stimuli were presented synchronously. Bottom: schematic illustration of the visual and auditory target trials. Here the movement streams contained deviants in the middle of the movement, which served as targets. During multisensory target presentation the onset and offset of the deviants were synchronized between the modalities.