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Sounds facilitate visual motion discrimination via the enhancement of late occipital visual representations

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ABSTRACT

Sensory discriminations, such as judgements about visual motion, often benefit from multisensory evidence. Despite many reports of enhanced brain activity during multisensory conditions, it remains unclear which dynamic processes implement the multisensory benefit for an upcoming decision in the human brain. Specifically, it remains difficult to attribute perceptual benefits to specific processes, such as early sensory encoding, the transformation of sensory representations into a motor response, or to more unspecific processes such as attention. We combined an audio-visual motion discrimination task with the single-trial mapping of dynamic sensory representations in EEG activity to localize when and where multisensory congruency facilitates perceptual accuracy. Our results show that a congruent sound facilitates the encoding of motion direction in occipital sensory - as opposed to parieto-frontal - cortices, and facilitates later - as opposed to early (i.e. below 100 ms) - sensory activations. This multisensory enhancement was visible as an earlier rise of motion-sensitive activity in middle-occipital regions about 350 ms from stimulus onset, which reflected the better discriminability of motion direction from brain activity and correlated with the perceptual benefit provided by congruent multisensory information. This supports a hierarchical model of multisensory integration in which the enhancement of relevant sensory cortical representations is transformed into a more accurate choice.

1. Introduction

Multisensory integration can improve perceptual performance across a wide range of tasks. While there is an emerging consensus that the underlying neural correlates likely involve multiple stages of the sensory decision making pathways, it remains a challenge to uncover the dynamic processes that implement the multisensory benefit for an upcoming decision in the human brain (Bizley et al., 2016; Kayser and Shams, 2015; Rohe and Noppeney, 2014, 2016). For example, many studies have shown that judgements about visual motion can be influenced by simultaneous sounds (Alais and Burr, 2004; Beer and Roder, 2004; Lewis and Noppeney, 2010; Schmiedchen et al., 2012) or vestibular information (Fetsch et al., 2010; Gu et al., 2008), even so when the multisensory stimulus is not directly task relevant (Gleiss and Kayser, 2014b; Kim et al., 2012; Sekuler et al., 1997). In particular, congruent multisensory evidence enhances visual motion discrimination performance over incongruent multisensory information (Meyer and Wuerger, 2001; Meyer et al., 2005; Soto-Faraco et al., 2003; Soto-Faraco et al., 2002). Yet, it remains difficult to attribute these perceptual benefits to specific neural processes, such as the encoding of visual motion in occipital cortices, the transformation of sensory representations into a motor response in parieto-frontal regions, or to more unspecific changes in sensory-response gain such as attentional effects (Beer and Roder, 2004; Bizley et al., 2016; Lewis and Noppeney, 2010; Talsma et al., 2010).

Electrophysiological studies in monkeys have illustrated in great detail how neural populations in visual motion regions, such as the Medial Superior Temporal Area (MSTd), combine directional information from the visual and vestibular senses to yield a more precise and reliable estimate of the perceived motion direction (Fetsch et al., 2013; Fetsch et al., 2012; Gu et al., 2008). These neurons weigh the two sensory inputs in proportion to each senses reliability, in a similar way as the behavioural benefits arise from the combination of visual and vestibular information (Angelaki et al., 2009; Fetsch et al., 2009). While this could be taken to suggest that multisensory benefits for visual motion discrimination in the human brain are similarly arising from an enhancement of the encoding of visual motion in occipital regions, we still have a limited understanding of when and where the underlying neural processes operate. While fMRI studies support a central role of visual motion cortex in mediating multisensory benefits (Alink et al., 2008; Lewis and Noppeney, 2010; Scheef et al., 2009), studies on other tasks such as spatial localization have provided a more

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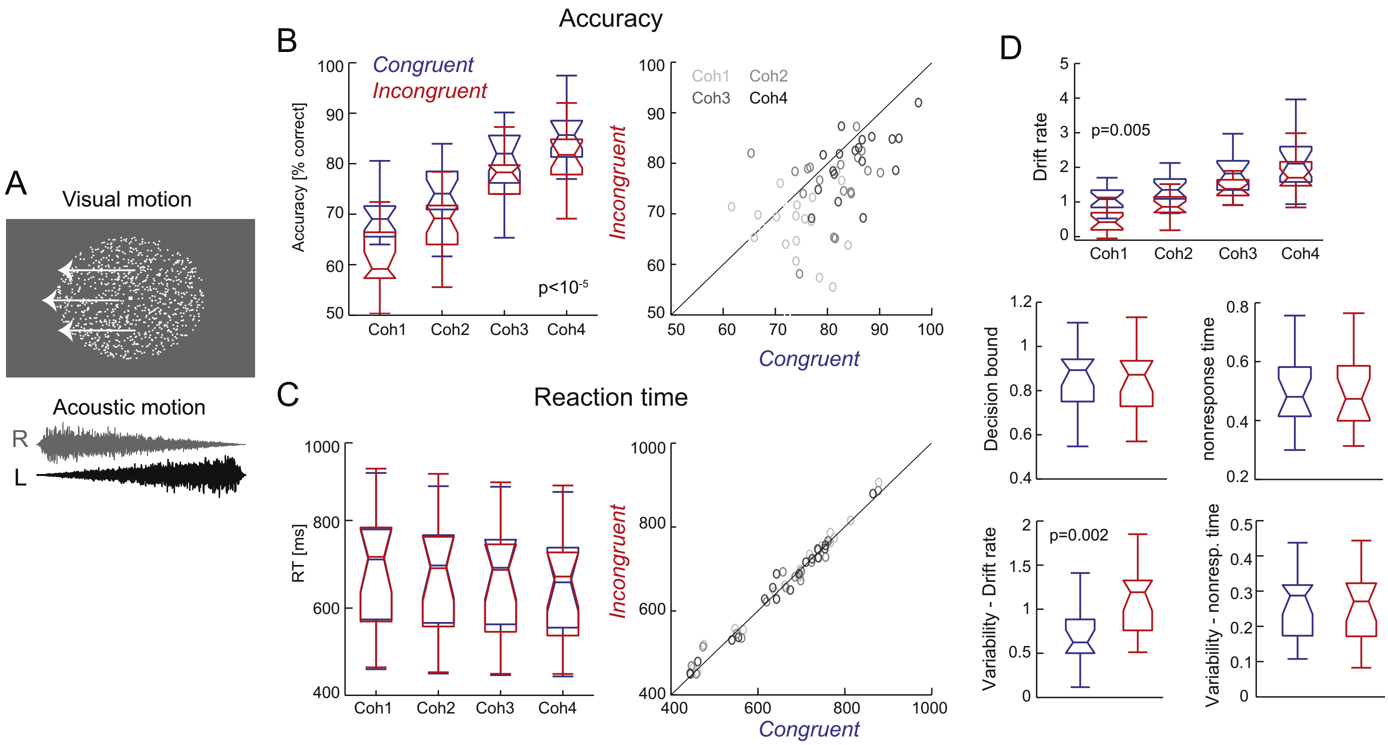

Fig. 1. Experimental paradigm and behavioural data. A) Subjects performed a speeded visual motion discrimination task (left- or right-wards). Random dot motion was presented at four coherence levels (coh 1–4) titrated around each participant's perceptual threshold. Visual stimuli were accompanied by acoustic motion implemented by changing levels of sound intensity between ears, either moving in the same (congruent) or opposite direction (incongruent) as the visual stimulus. B) Perceptual accuracy increased significantly with motion coherence and was significantly higher during congruent trials. C) Reaction times did not change significantly with coherence or congruency. D) Parameters derived from drift-diffusion models fit to behavioural data, with significant congruency effects in drift rates and their variability. Variability = Inter-trial variability. Boxplots: medians and percentiles across participants (n=18).

nuanced picture, one in which multiple occipital and parietal regions contribute distinctively to multisensory integration (Rohe and Noppeney, 2014, 2016). For example, while studies using planar motion have implied the hMT complex (but see (Baumann and Greenlee, 2007)), a study on motion in depth has pointed to a role of area V3A (Ogawa and Macaluso, 2013) and regions within the IPS (Guipponi et al., 2013). Given the frequent focus on mapping activations rather than sensory representations (Kriegeskorte et al., 2006), and given that many prior studies have relied on the relatively slow fMRI-BOLD response, these studies do not provide a detailed understanding of where and when during a trial perceptually relevant multisensory benefits emerge and are transformed into perceptual benefits on a single trial basis (Bizley et al., 2016; Zhang et al., 2016).

Exploiting the temporal resolution of EEG or MEG, a few studies have investigated the neural mechanisms of audio-visual interactions in the context of motion perception. Studies focusing on auditory cortical activity have shown that the congruency of visual information can affect auditory brain activity already at latencies of around 100 ms (Stekelenburg and Vroomen, 2009; Zvyagintsev et al., 2009) while occipital evoked responses were affected by cross-modal attention around 200 ms post-stimulus onset (Beer and Roder, 2005), and occipital oscillatory activity was affected by Audio-visual motion congruency already around 100 ms (Gleiss and Kayser, 2014b). However, these EEG/MEG studies also focused on mapping generic activations rather than mapping sensory representations, and the use of trial-averaged activity made it difficult to link neural mechanisms to the perceptual single trial benefits.

We hence reasoned that EEG-based neuroimaging combined with the single trial mapping of task-relevant sensory representations could provide important insights about the neural processes mediating the multisensory enhancement of motion discrimination. In particular we exploited an information-mapping approach, in which we used single trial decoding to select EEG activations that are relevant to the subjects' behaviour and task, rather than studying single electrode ERPs. Our specific aims were to test whether acoustic information enhances the quality of early or later visual representations in occipital cortex, or manifests mostly in decision-related processes in parieto-frontal regions and immediately before the response. To this end we combined a standard motion discrimination task with single-trial EEG analysis to map the relevant dynamic representations of visual motion direction. We then asked when in time during a trial EEG activations carrying the task-relevant visual information were modulated by multisensory congruency and whether these activations localized to sensory cortices, or fronto-parietal association regions.

To better understand the potential role of attention-related processes in multisensory perception we also extracted parietal alpha activity and related this to the observed behavioural benefits and the neural encoding processes. The power of parietal alpha has been linked to visual spatial attention and the excitability of visual cortices (Romei et al., 2010; Thut et al., 2006; VanRullen, 2016), with higher (lower) power being potentially indicative of reduced (increased) attentional focus. As previous work has suggested that alpha power can change with multisensory congruency (Gleiss and Kayser, 2014b), we sought to replicate this effect, and to test whether a change in alpha band activity contributes to multisensory perceptual benefits at the single trial level, for example by modulating the contribution of sensory information to perceptual choice.

2. Materials and methods

Data were obtained from 18 healthy adult participants (8 males; mean age of 21.3 years) following written informed consent and briefing about the purpose of the study. All had self-reported normal hearing and vision, declared no previous history of neurological