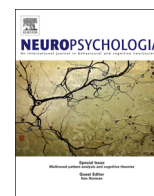




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# Oscillatory mechanisms underlying the enhancement of visual motion perception by multisensory congruency

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## ABSTRACT

Multisensory interactions shape every day perception and stimuli in one modality can enhance perception in another even when not being directly task relevant. While the underlying neural principles are slowly becoming evident, most work has focused on transient stimuli and little is known about those mechanisms underlying audio–visual motion processing. We studied the facilitation of visual motion perception by auxiliary sounds, i.e. sounds that by themselves do not provide the specific evidence required for the perceptual task at hand. In our experiment human observers became significantly better at detecting visual random dot motion when this was accompanied by auxiliary acoustic motion rather than stationary sounds. EEG measurements revealed that both auditory and visual motion modulated low frequency oscillations over the respective sensory cortices. Using single trial decoding we quantified those oscillatory signatures permitting the discrimination of visual motion similar to the subject's task. This revealed visual motion-related signatures in low (1–4 Hz) and alpha (8–12 Hz) bands that were significantly enhanced during congruent compared to disparate audio–visual conditions. Importantly, the auditory enhancement of these oscillatory signatures was predictive of the perceptual multisensory facilitation. These findings emphasise the importance of slow and alpha rhythms for perception in a multisensory context and suggest that acoustic motion can enhance visual perception by means of attention or priming-related mechanisms that are reflected in rhythmic activity over parieto-occipital regions.

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## 1. Introduction

Stimuli presented to one modality can enhance our perceptual performance in detecting or discriminating stimuli in another, even without providing information about the task relevant feature. For example, a tone can improve the detection of dim lights (Chen, Huang, Yeh, & Spence, 2011; Lippert, Logothetis, & Kayser, 2007; McDonald, Teder-Salejarvi, & Hillyard, 2000; Noesselt et al., 2010) or facilitate the search for dynamic visual targets (Van der Burg, Olivers, Bronkhorst, & Theeuwes, 2008). Similar effects occur for other combinations of sensory modalities (Jaekl & Soto-Faraco, 2010; Lovelace, Stein, & Wallace, 2003; Thorne & Debener, 2008), can be specific to task instructions or stimulus eccentricity (Chen et al., 2011; Gleiss & Kayser, 2013; Jaekl & Soto-Faraco, 2010; Leo, Bertini, di Pellegrino, & Ladavas, 2008), and may relate to mechanisms based on attentional capture or stimulus-triggered changes in sensory gain (Chen et al., 2011;

Lippert et al., 2007). While many studies on auxiliary multisensory benefits focus on brief or stationary stimuli, considerably less is known about the interaction of auditory and visual motion.

Previous work has shown that both moving and stationary sounds can affect the precision or quality of a visual motion percept, also when the sound is not of primary relevance for the task at hand. For example, brief sounds can alter bi-stable visual motion precepts (Sekuler, Sekuler, & Lau, 1997) and task-irrelevant acoustic motion can enhance visual motion detection (Kim, Peters, & Shams, 2012). Other work has shown that audio–visual motion features can combine for a general perceptual enhancement (Alais & Burr, 2004; Senkowski, Saint-Amour, Kelly, & Foxe, 2007; Wuerger, Hofbauer, & Meyer, 2003) or more specific feature integration (Harrison, Wuerger & Meyer, 2010; Lopez-Moliner & Soto-Faraco, 2007; Meyer, Wuerger, Rohrbein, & Zetzsche, 2005). This suggests that auditory and visual motion evidence interact in different ways and experimental contexts (see also (Cappe, Thelen, Romei, Thut, & Murray, 2012; Senkowski et al., 2007)). In search for an underlying neural substrate functional imaging studies localised brain areas mediating the integration of acoustic and visual motion evidence (Alink, Singer, & Muckli, 2008; Guipponi et al., 2013; Lewis & Noppeney, 2010; Scheef et al., 2009). However, the specific neural mechanisms underlying

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a sound driven enhancement of visual motion detection remain poorly understood.

To link perceptual multisensory benefits with the neural processing of visual motion we studied a paradigm in which sounds enhance the subject's accuracy in identifying coherent visual motion without providing direct evidence that would allow solving the perceptual task based on just the acoustic evidence (Kim et al., 2012). Specifically, we used a 2-interval forced choice paradigm in which subjects had to identify which of two intervals contained coherent visual motion. The auditory stimulus was the same during both intervals and by itself did not identify the stimulus interval containing coherent visual motion. However, on half the trials the sound provided congruent motion information that could enhance visual motion processing and hence the perceptual performance.

Our hypothesis about the neural mechanisms underlying the perceptual multisensory benefit in this task was based on recent suggestions for a prominent role of oscillatory brain activity in mediating multisensory interactions (Schroeder & Lakatos, 2009; Schroeder, Lakatos, Kajikawa, Partan, & Puce, 2008). Experimental support for this has been found in different brain areas and paradigms (Bauer, Oostenveld, & Fries, 2009; Fiebelkorn et al., 2011; Gomez-Ramirez et al., 2011; Kayser, Petkov, & Logothetis, 2008; Lakatos et al., 2009; Mercier et al., 2013; Thorne, De Vos, Viola, & Debener, 2011). For example, several studies found that brief and transient sounds can shape the amplitude and phase of oscillatory activity over occipital areas (Naue et al., 2011) and that this modulation of low frequency oscillations directly relates to perceptual performance in visual tasks (Romei, Gross, & Thut, 2012; Romei, Murray, Cappe, & Thut, 2009; Thut, Miniussi, & Gross, 2012). We hence hypothesised that similar oscillatory mechanisms may underlie an auditory driven enhancement of visual motion perception. We directly tested this hypothesis using methods of single trial decoding to link stimulus related oscillatory signatures with multisensory perceptual benefits.

## 2. Materials and methods

### 2.1. General experimental procedures

Adult volunteer subjects (aged 18–35, both sexes) were paid to participate in the experiments. All reported normal hearing, normal or corrected to normal vision

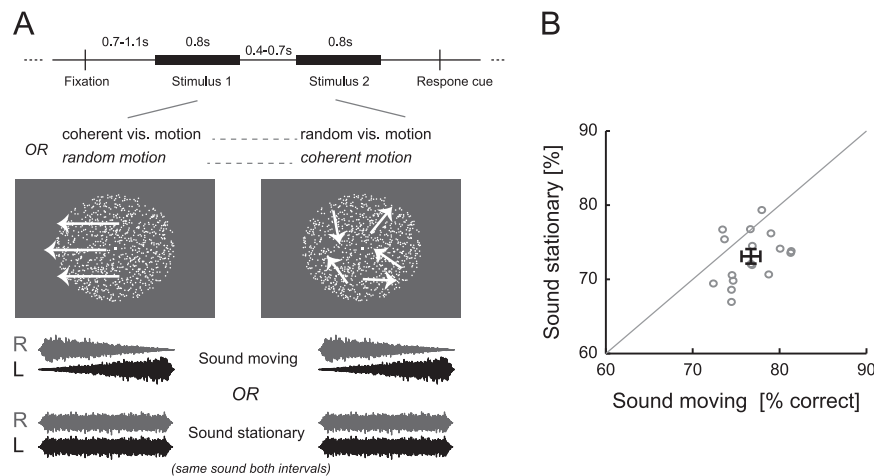
and gave written informed consent prior to participation. The experiments were conducted according to the Declaration of Helsinki and were approved by the joint ethics committee of the University Clinic and the Max Planck Institute for Biological Cybernetics Tübingen. Experiments were performed in a sound-attenuated and dark room. Visual stimuli were presented on a gamma-corrected monitor (24", 60 Hz) positioned 57 cm from the subject's head, while acoustic stimuli were presented binaurally using a Sennheiser In-Ear headphone (Model PMX 80). Stimulus presentation was controlled from Matlab (Mathworks) using routines from the Psychophysics toolbox (Brainard, 1997; Pelli, 1997). Sound levels were calibrated using a condenser microphone (Bruel&Kjaer 4188) and a sound level metre (2238 Mediator; Bruel&Kjaer). The subjects head was stabilized using a chin-rest and they used a computer keyboard to indicate their responses. We obtained data from  $n=19$  subjects, but data from two subjects had to be discarded because of either excessive line noise or artefacts. Reported results are from  $n=17$  subjects.

### 2.2. Behavioural task and stimuli

The rationale of the task was to study how auxiliary and not primarily task relevant (i.e. necessary) sounds affect visual motion detection. To this end we implemented a challenging visual motion detection task based on random dot stimuli in a two interval forced choice procedure (Fig. 1A). This task required subjects to indicate which of two stimulus intervals contained coherent visual motion (only one did), with the level of visual motion coherence being selected for each subject to obtain intermediate (~75% correct) levels of performance. To test the impact of auditory motion evidence on this task we presented the visual stimuli in a multisensory context. During each trial the same acoustic stimulus, either an unambiguously moving or a stationary sound, was presented during both visual stimuli. Consequently the sound did not offer direct evidence to perform the task; i.e. the task could not be solved based on just the acoustic stimulus. However, on those trials where the sound was moving in the same direction as the coherent visual motion, the sound provided multisensory contextual information that could facilitate performance. As a result of this design all stimuli were multisensory and no unisensory trials were employed.

The random dot patterns were presented following the onset of a fixation dot (0.7–1.1 s uniform delay), lasted each for 0.8 s and were separated by a random delay (0.4–0.7 s; Fig. 1A). Subsequently to the second stimulus (0.2–0.5 s) a question mark appeared cuing subjects to respond. Subjects had to indicate which of the two intervals contained the coherent visual motion, and they had to do so by pressing 'up' (for the 1st interval) or 'down' (for the 2nd) arrow keys on a keyboard. This ensured a response assignment that is orthogonal to stimulus sequence. Individual trials were separated by 1.5–2 s intervals and subjects were instructed to respond 'as accurately as possible'. Trials were presented in blocks of 160 trials and each subject performed 6 blocks. The order of stimulus intervals (containing or random) motion was randomized. Given the nature of a two interval forced choice task behavioural performance was analysed using the percentage correct responses and reaction times were not assessed (Green & Sets, 1966).

Random dot patterns (1400 dots, white) were centred on the fixation spot, covered 15° of visual angle (with the centre 1° devoid of dots) and were presented on a neutral grey screen (3 cd/m<sup>2</sup> background luminance). Individual dots were 0.2° large, moved at 9°/s in a random direction and 8% of dots were randomly replaced after each frame (16 ms). In one of the two dot patterns in each trial a



**Fig. 1.** Behavioural paradigm and results. (A) Random dot stimuli were presented in a two interval paradigm, whereby one stimulus contained only random motion while the other contained coherent left- or right-wards motion. Subjects fixated on a central dot and had to indicate which of the two intervals contained coherent motion by a button press. In a given trial the same sound was presented during both stimulus intervals. This sound could be either a stationary white noise ('sound stationary'), or amplitude modulated noise ('sound moving') creating an unambiguous motion percept in the same direction as the visual motion. Direction of motion, motion interval and sound conditions were randomized on a trial by trial basis. (B) Scatter plot showing single subject performance (% correct responses) and mean values (mean and standard error; cross-hair) for trials with stationary and moving sounds. Subjects ( $n=17$ ) performed significantly better during the moving sound (paired  $t$ -test,  $p < 0.001$ ).

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