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The influence of spontaneous brain oscillations on apparent motion perception

Lia Lira Olivier Sanders [a,1], Ryszard Auksztulewicz [a,b,*,1,2], Friederike U. Hohlefeld [c], Niko A. Busch [a,d], Philipp Sterzer [a,e]

[a] Berlin School of Mind and Brain, Humboldt-Universität zu Berlin, Luisenstraße 56, Haus 1, 10117 Berlin, Germany
[b] Wellcome Trust Centre for Neuroimaging, Institute of Neurology, University College London, 12 Queen Square, WC1N 3BG London, UK
[c] Neurophysics Group, Department of Neurology and Clinical Neurophysiology, Charité University Medicine Berlin, Hindenburgdamm 30, 12200 Berlin, Germany
[d] Institute of Medical Psychology, Charité University Medicine, Luisenstr. 57, 10117 Berlin, Germany
[e] Charité University Medicine, Department of Psychiatry, Campus Charité Mitte, Charitéplatz 1, 10117 Berlin, Germany

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A B S T R A C T

A good example of inferential processes in perception is long-range apparent motion (AM), the illusory percept of visual motion that occurs when two spatially distinct stationary visual objects are presented in alternating sequence. The AM illusion is strongest at presentation frequencies around 3 Hz. At lower presentation frequencies, the percept varies from trial to trial between AM and sequential alternation, while at higher frequencies perception varies between AM and two simultaneously flickering objects. Previous studies have demonstrated that prestimulus alpha oscillations explain trial-to-trial variability in detection performance for visual stimuli presented at threshold. In the present study, we investigated whether fluctuations of prestimulus alpha oscillations can also account for variations in AM perception. Prestimulus alpha power was stronger when observers reported AM perception in subsequent trials with low presentation frequencies, while at high presentation frequencies there were no significant differences in alpha power preceding AM and veridical flicker perception. Moreover, when observers perceived AM the prestimulus functional connectivity between frontal and occipital channels was increased in the alpha band, as revealed by the imaginary part of coherency, which is insensitive to artefacts from volume conduction. Dynamic causal modelling of steady-state responses revealed that the most likely direction of this fronto-occipital connectivity was from frontal to occipital sources. These results point to a role of ongoing alpha oscillations in the inferential process that gives rise to the perception of AM and suggest that fronto-occipital interactions bias perception towards internally generated predictions.

Introduction

The inferential nature of perception becomes evident when fragmented sensory inputs evoke the illusory filling-in of perceptual features (Gregory, 1997). A good example of such perceptual inference is long-range apparent motion (AM) (Tse and Cavanagh, 2000). This illusion occurs when two spatially separated stimuli are presented in rapid succession, leading to the perception of a single moving stimulus (Wertheimer, 1912). The illusory motion percept is thought to reflect the best perceptual solution of the problem posed by the rapid alternating appearance and disappearance of the stationary stimuli (Sigman and Rock, 1974). AM is strongest at an alternation rate of ≈3 Hz (Finlay and von Grunau, 1987). At lower presentation frequencies, the percept varies from trial to trial between sequential alternation and smooth movement (AM). At higher frequencies, perception fluctuates between AM and two simultaneously flickering dots (Fig. 1A). However, it is unclear which neural processes are responsible for this trial-to-trial variability in perception.

Previous studies have suggested that cortico-cortical synchronisation in the alpha band mediates top-down influence on sensory information processing (Haegens et al., 2011; Min and Herrmann, 2007; Min and Park, 2010; von Stein et al., 2000). Alpha oscillatory activity is thought to modulate sensory processing (Klimesch et al., 2007) by favouring expectation-driven, prediction-based operations over an external sensory input (Cooper et al., 2003; Ray and Cole, 1985). This is in line with the evidence that the amplitude (Babiloni et al., 2006; Ergenoglu et al., 2004; Thut et al., 2006; Worden et al., 2000) and phase (Busch and VanRullen, 2010; Busch et al., 2009; Dugue et al., 2011; Mathewson et al., 2009; Varela et al., 1981) of ongoing alpha oscillations just before stimulus onset influence detection of upcoming

* Corresponding author at: Wellcome Trust Centre for Neuroimaging, Institute of Neurology, University College London, 12 Queen Square, WC1N 3BG London, UK.
[1] These authors contributed equally to this work.
[2] Permanent address: Wellcome Trust Centre for Neuroimaging, Institute of Neurology, University College London, 12 Queen Square, WC1N 3BG London, UK.

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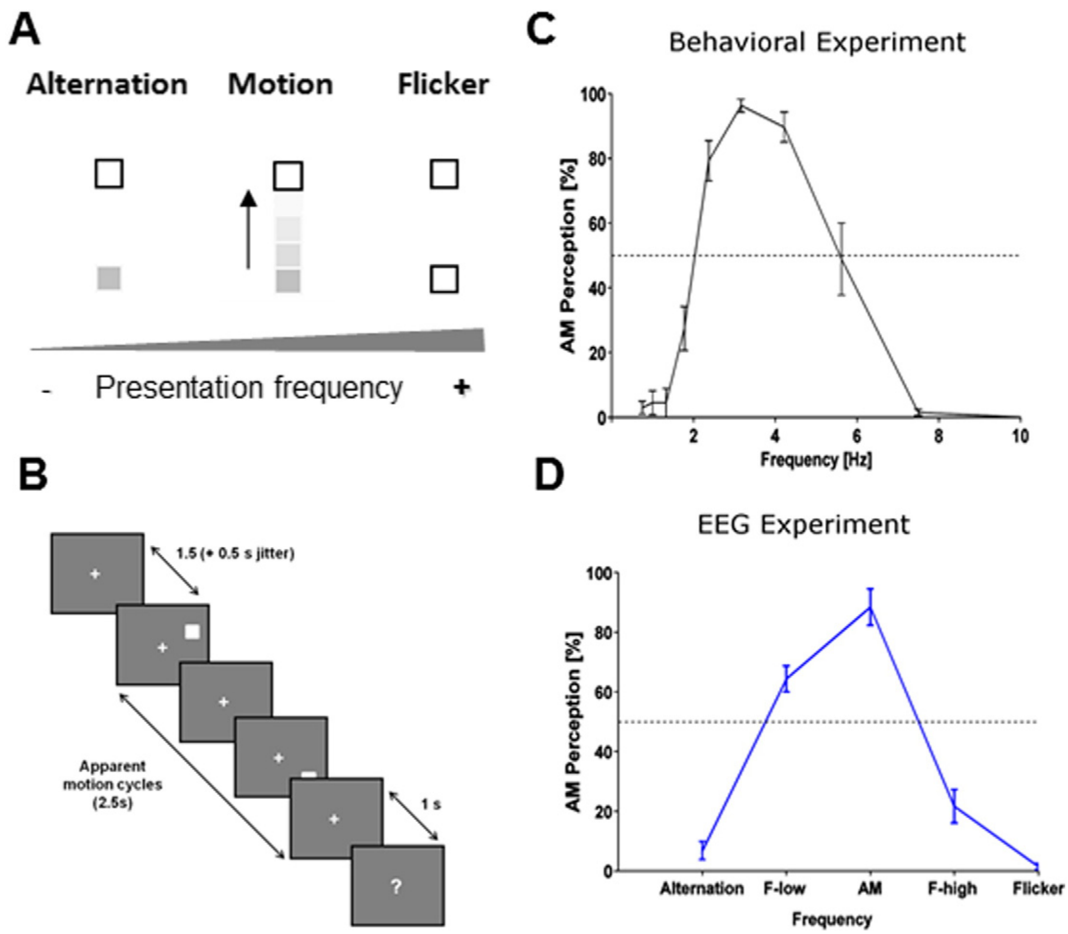

Fig. 1. Experimental procedure and behavioural responses. A) Schematic representation of apparent motion illusion. As the presentation frequency of peripheral visual stimulus increases, the percept changes from sequential alternation, to apparent motion, to flicker. B) Schematic representation of a single trial (EEG experiment). C) AM perception as a function of presentation frequency in the behavioural experiment and D) as a function of experimental condition (the two threshold frequencies at which reports fluctuated across trials between "alternation" and "motion" (F-low) and "motion" and "flicker" (F-high) as well as presentation frequencies with most consistent reports of "alternation", "AM", and "flicker") in the EEG experiment. Error bars represent ± 1 SEM.

visual stimuli. Here we reasoned that such an internally-oriented, top-down brain state that *impairs* detection of external stimuli might actually *facilitate* perception of visual illusions driven by internal predictions, such as AM (Alink et al., 2010; Sanders et al., 2012; Schwiedrzik et al., 2007; Sterzer et al., 2006). Therefore, our primary hypothesis was that strong prestimulus power (indicating local neural synchronisation; Schnitzler and Gross, 2005) of alpha oscillations would favour AM perception. In addition, given the evidence that long-distance alpha (8–12 Hz) phase coherence between the prefrontal and visual cortices may serve as a mechanism underlying anticipatory, top-down modulation (Zanto et al., 2010, 2011), we asked whether high prestimulus coherence (also termed functional connectivity; Friston, 1994) and its directionality (effective connectivity; Friston, 1994) in the alpha band between frontal and occipital regions might also be associated with the perception of AM.

Using two stimulation frequencies at which subjective perception fluctuated across trials between motion and alternation (low presentation frequency) or motion and flicker (high presentation frequency), we asked participants to report their percepts, while we recorded EEG signals. By comparing "motion perceived" and "motion not perceived" trials at each of the two presentation frequencies with respect to the prestimulus alpha power and functional connectivity between frontal and occipital channels, we found evidence for the modulation of AM perception by prestimulus alpha power and by fronto-occipital functional and effective connectivity.

Materials and methods

Participants

Fourteen subjects enrolled in the study after giving written informed consent. All of them had normal or corrected-to-normal vision. Two participants who did not perceive more than 50% AM at any presentation frequency did not take part in the main experiment. Two other participants were excluded from the analysis due to insufficient number of "motion perceived" trials after artefact rejection (out of the range of group mean ± 1 SD). The final sample consisted of ten subjects (4 females, mean age 26.8 ± 3.9 SD). This study was approved by the Charité University Medicine ethical committee.

Stimuli and procedure

The experiment was programmed in MATLAB (http://www.mathworks.com/) using the Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). Stimuli were presented on a CRT computer monitor (1280 × 1024 resolution, 100 Hz refresh rate, grey background). Participants were seated in front of the screen in a darkened room (48 cm viewing distance). A trial started with the presentation of a fixation cross for 500 ms (behavioural experiments) or 1500 ms + 500 ms jitter (EEG experiment; see Fig. 1B), followed by AM stimuli, which consisted of white squares (2.35° × 2.35°) flashed