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Cortical oscillatory activity associated with the perception of illusory and real visual contours

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ABSTRACT

We used magnetoencephalography (MEG) to examine the nature of oscillatory brain rhythms when passively viewing both illusory and real visual contours. Three stimuli were employed: a Kanizsa triangle; a Kanizsa triangle with a real triangular contour superimposed; and a control figure in which the corner elements used to form the Kanizsa triangle were rotated to negate the formation of illusory contours. The MEG data were analysed using synthetic aperture magnetometry (SAM) to enable the spatial localisation of task-related oscillatory power changes within specific frequency bands, and the time-course of activity within given locations-of-interest was determined by calculating time-frequency plots using a Morlet wavelet transform. In contrast to earlier studies, we did not find increases in gamma activity (>30 Hz) to illusory shapes, but instead a decrease in 10–30 Hz activity approximately 200 ms after stimulus presentation. The reduction in oscillatory activity was primarily evident within extrastriate areas, including the lateral occipital complex (LOC). Importantly, this same pattern of results was evident for each stimulus type. Our results further highlight the importance of the LOC and a network of posterior brain regions in processing visual contours, be they illusory or real in nature. The similarity of the results for both real and illusory contours, however, leads us to conclude that the broadband (<30 Hz) decrease in power we observed is more likely to reflect general changes in visual attention than neural computations specific to processing visual contours.

1. Introduction

Illusory contours can be perceived in conditions where feature edges are aligned but do not physically join, as is evident in the classic Kanizsa Triangle in Fig. 1 (Kanizsa, 1976). However, the cortical operations involved in processing illusory contours and how they relate to neural processing of real visual contours remains unclear. Multi-unit recordings in animals (Eckhorn et al., 2004), EEG (Tallon-Baudry et al., 1997) and biomagnetic recordings in human (Kaiser et al., 2004) provide evidence to suggest that cortical oscillatory activity within local and distributed neuronal assemblies may be important for processing contours (e.g. Singer, 1999). At macroscopic levels of measurement (EEG/MEG), one assumes that increases in the power of the aggregate signal generally denote synchronization of the underlying network whereas decreases in the power generally reflect desynchronization (Pfurtscheller and Lopes da Silva, 1999). Synchronous neuronal responses have been attributed to the process of feature binding (Buzsaki, 2005; Seghier and Vuilleumier, 2006), while the importance of desynchronous oscillatory activity in segmenting different cognitive moments has also been discussed (Breakspear et al., 2004). Within early visual areas, there is evidence that oscillatory activity in the gamma frequency band supports illusory contour processing (Tallon-Baudry et al., 1996; Kaiser et al., 2004), perhaps linked to processes involved with increased attention towards a visual target (Herrmann and Mecklinger, 2000; Halgren et al., 2003; Kaiser et al., 2004; Vidal et al., 2006).

Focal reductions in the power of low-frequency oscillations (<30 Hz) have also been implicated in visual processing, with several reports that coherent object perception (Maratos et al., 2007) is associated with reductions in power within the beta frequency range (13–30 Hz). Additionally, theta activity (4–8 Hz) has been linked to gamma and may represent a general mechanism for phase coding needed to bind disparate populations of neurons (O'Keefe and Recce, 1993; Fries et al., 2007; Jacobs et al., 2007).

A recent model of illusory contour processing suggests boundary completion takes place in the lateral occipital complex (LOC) (Murray et al., 2002; Murray et al., 2006). Single-cell recordings in animal studies, however, show that some neurons in cortical areas V1 and V2 also respond when illusory contours move across their receptive fields (von der Heydt and Peterhans, 1989; Sheth et al., 1996). In support of this, human fMRI (functional magnetic resonance imaging) studies have reported increased BOLD (blood oxygenation level-dependant)

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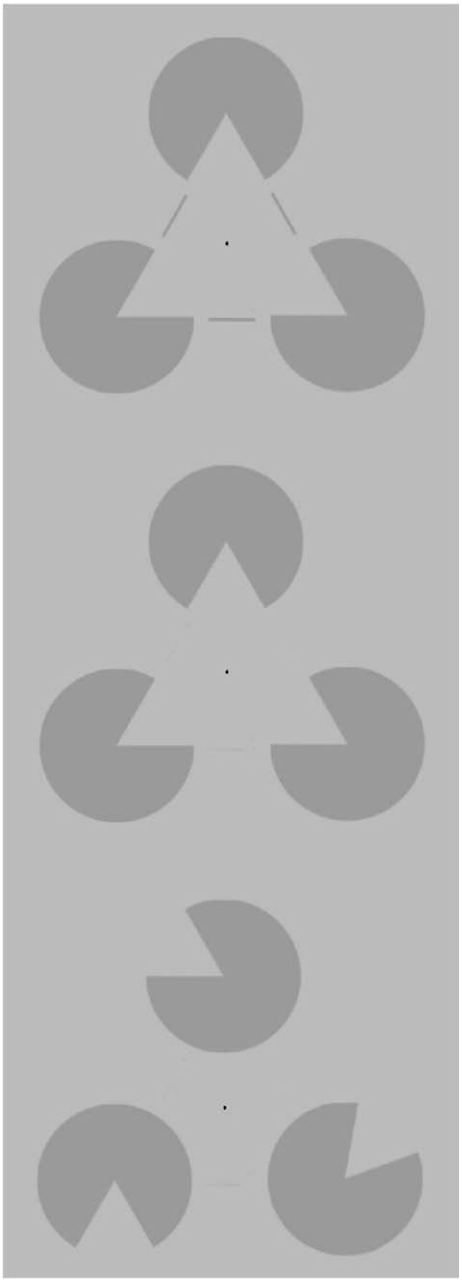

Fig. 1. Example of real triangle (top), illusory triangle (middle) and non-triangle stimulus employed.

responses in area V1 following the perception of illusory contours, though it remains unclear whether some or all of this activity reflects feedback projections from the LOC (Seghier et al., 2000; Halgren et al., 2003).

In this study, we examined neural response patterns related to the perception of real and illusory contours, seeking to further understand the role oscillatory brain rhythms may play in binding visual features. We used a stimulus paradigm based on the Kanizsa illusory triangle figure and analysed the MEG data using a beamformer approach termed synthetic aperture magnetometry (SAM) (Barnes and Hillebrand, 2003; for a review see Hillebrand and Barnes, 2005). For a more detailed description of the beamformer algorithm, see Appendix A. This approach allows for the measure of task-related cortical oscillatory power changes within specific frequency bands, and is ideally suited for both the spatial and temporal characterisation of neuronal responses (Van Veen et al., 1997; Taniguchi et al., 2000; Vrba and Robinson, 2001; Singh et al., 2002; Barnes and Hillebrand, 2003; Cheyne et al., 2003; Singh et al., 2003; Hillebrand et al., 2005). Our main aims were to: a) provide further evidence for the reported role of enhanced gamma activity during the perception of illusory contours; and b) determine whether other brain rhythms, and in particular beta activity, are affected during the perception of real and/or illusory contours, and if so determine their cortical distribution.

2. Methods

2.1. Participants

Twelve healthy adult participants (8 male and 4 female) between the ages of 25 and 55 with no history of neurological disorders were recruited. All participants had normal or corrected-to-normal vision. The study was undertaken with the understanding and written consent of each participant, conformed with The Code of Ethics of the World Medical Association (Declaration of Helsinki), and was granted ethical approval by the Aston University Human Sciences Ethical Committee.

2.2. Procedure and stimuli

Participants were presented with three dark grey circles on a light gray background with a Michelson contrast of 17% [$C_{\mathrm{m}} = (L_{\mathrm{max}} - L_{\mathrm{min}} / L_{\mathrm{max}} + L_{\mathrm{min}}) \times 100$], which was suprathreshold but sufficiently low to avoid troublesome after-images. A small wedge was removed from each circle to yield an inducer element (sometimes termed ‘pacman’

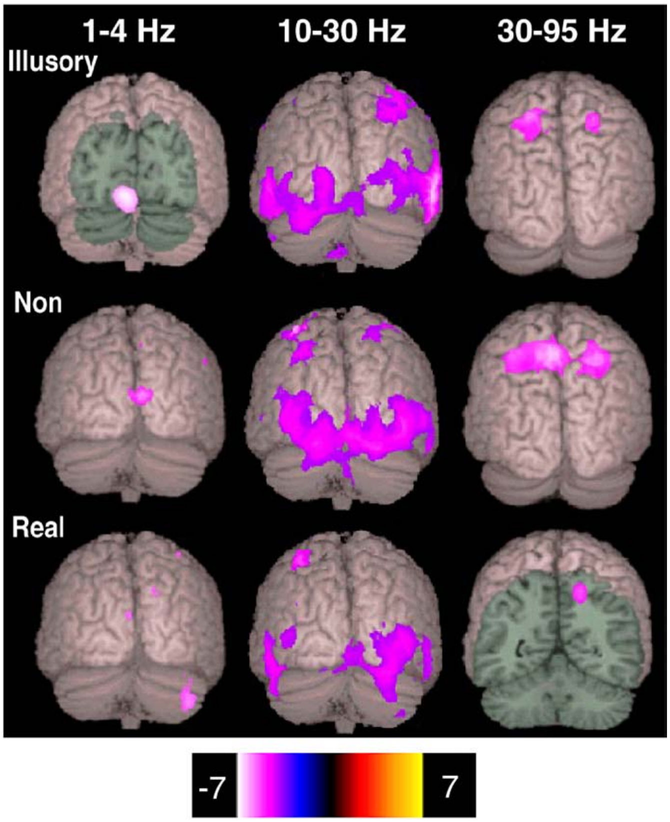

Fig. 2. Surface rendered group SAM images of the posterior brain depicting statistical estimates ($p < 0.05$) of power changes within the 1–4 Hz, 10–30 Hz and 30–95 Hz frequency bands between active and passive experimental states (500 ms) for viewing the illusory triangle (top), non-triangle pattern (middle) and real triangle pattern (bottom). The colour scale shows pseudo-*t* values for the oscillatory power changes: white-purple colours indicate a relative decrease in signal power during the active phase, while yellow–orange colours indicate a relative increase.