



Frontal theta activity is pronounced during illusory perception



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ABSTRACT

Object perception is driven by sensory information as well as expectations and prior experiences. The latter influence may increase when the sensory information is poor or inconclusive. Visual illusions, for example induced by ambiguous stimuli, provide a tool to investigate perceptual uncertainty, because ambiguous stimuli elicit switching between at least two perceptual alternatives. Theta oscillations may reflect the impact of visual illusion on perception since they are specifically important to coordinate information in large-scale brain networks, including visual sensory as well as higher-order brain areas. Theta responses elicited by an *ambiguous* and an *unambiguous* apparent motion-inducing stimulus were compared, thereby differentiating time periods of perceptual *switching* and perceptual *stability (non-switching)*. The theta responses were larger at anterior than at posterior sites. This gradient was stronger during the *ambiguous* task than during the *unambiguous* task, even though sensory stimulation was comparable for both tasks. A transient increase of the theta response occurred during *switching* time periods for both the *ambiguous* and the *unambiguous* tasks, indicating that the theta response related to the perceptual switch might not be affected by the ambiguity of the stimulus. Irrespective of the percept switching or not, ambiguous stimuli elicited an enduring more prominent activation of higher-order rather than visual sensory brain areas. This indicates an increased reliance on expectations and prior information to ensure coherent object perception in particular when the visual information is degraded or elicits an ongoing conflict between perceptual interpretations.

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1. Introduction

Watching clouds in the summer sky often leads to the experience of meaningful objects, faces or animals slowly emerging, re-shaping and dissolving. This experience may reveal the imperative of our neural system to create a coherent flow of action-guiding perceptual experiences from the sensory information provided by the external surroundings. Fast integration of bottom-up (sensory-driven) and top-down (expectation- and memory-driven) processes serve this goal by comparing stimulus-driven input with prior experience, by bridging sensory information gaps and by guiding the attentional focus towards behaviourally relevant information (Albright, 2012; Fuster, 2009; Miller et al., 2011; Murray and Herrmann, 2013).

Ambiguous stimuli elicit a special case of object perception. The sensory information is inconclusive regarding the generation of a coherent percept, because more than one meaningful solution is similarly probable to account for the current percept. In order to maintain perceptual coherence only one perceptual alternative at a time is perceived. During

continuous observation, perception switches between all possible alternatives although the physical properties remain unchanged (Long and Toppino, 2004).

The aim of the current study was to investigate the modulation of the neural response reflecting coherent object perception under constraints of visual multistability. We hypothesised that ambiguous stimuli elicit an increased activation of top-down processes. This may become apparent in large-scale networks, including early sensory as well as higher-order brain areas.

The involvement of large-scale networks of the brain in multistable perception might be observed best in the oscillatory theta response, because theta activity has been linked to the general capacity of the brain to transfer and coordinate information over large distances (von Stein and Sarnthein, 2000), to bind neural assemblies of different brain areas (Lopes da Silva, 2013) and to integrate sensory information over prolonged time periods (Kayser et al., 2012). Consequently, theta activity and most often the modulation of its fronto-medial maximum has been reported to reflect various cognitive functions, such as focussed attention (Basar-Eroglu et al., 1992; Polich, 2007), long-term and working memory (Klimesch et al., 2010; Polich, 2007; Sauseng et al., 2010), imagination (de Borst et al., 2012), utilisation of prior knowledge for visual integration (Volberg et al., 2013b), handling of conflicts (Cohen and Cavanagh, 2011) and action control (Huster et al., 2013; Schmiedt-Fehr and Basar-Eroglu, 2011; Schmiedt-Fehr et al., 2011; Yordanova et al.,

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2004). Anterior theta activity might control and influence posterior brain sites, including early visual areas (Cohen and van Gaal, 2013; de Borst et al., 2012; Lee and D'Esposito, 2012; Sauseng et al., 2006). Further, disturbances in anterior-posterior theta networks are reflective for deficits as known from patients with schizophrenia (Basar-Eroglu et al., 2008), dementia (Yener and Basar, 2010) and synesthesia (Volberg et al., 2013a).

Given the strong influences of cognitive functions, such as the observer's intention, on the current perception of an *ambiguous* stimulus (Mathes et al., 2006; Strüber and Stadler, 1999) it is surprising that the role of theta oscillations for *ambiguous* stimuli remains unclear and has been disregarded. Earlier studies reported an increase of theta activity around the perceptual switch in persons who frequently encounter perceptual switches (Nakatani and van Leeuwen, 2005). A similar result was reported for gamma activity (Strüber et al., 2000). Both findings may be related to the attention towards the task or the vigilance of the observer rather than to any specific requirements driven by the ambiguity of the task. The time course of the gamma activity, however, differs around the perceptual switch when the stimulus is *ambiguous* (Ehm et al., 2011). Strüber et al. (2014) have further shown that transcranial alternating current stimulation, which is thought to synchronise oscillations in the stimulated frequency range, increases gamma coherence and influences switching behaviour when applied over parieto-occipital sites. No such effect was observed for the theta band (Ehm et al., 2011; Strüber et al., 2014).

Theta activity serves multiple perceptual and cognitive functions (Basar, 2006) and, therefore, theta activity related to different aspects of the task may be superimposed. The reported results mainly focus on perceptual *switching*. The appearance of a task-relevant perceptual event, such as a perceptual switch, is known to elicit a transient increase in theta activity (Basar-Eroglu and Demiralp, 2001), which might dominate the brain response similarly for perceptual switches induced by *ambiguous* or *unambiguous* stimuli. Perception of *ambiguous* stimuli, however, elicits an ongoing active state of the brain (Basar-Eroglu et al., 1996a) and might affect time periods of perceptual *switching* as well as perceptual stability (*non-switching*). Theta activity related to multistable perception may, therefore, show an enduring characteristic (see also Gevins et al., 1997). Here, we investigated *switching* and *non-switching* time periods using both *ambiguous* and *unambiguous* stimuli (see *Stimuli and tasks* section, below, for a more detailed description and Müller et al., 2005 for the use of a similar analytical technique).

A newly developed strategy ensured sensitivity towards the sensory information, because we assumed that the difference between the *ambiguous* and *unambiguous* tasks would become apparent in the distribution of theta activation within large-scale networks integrating bottom-up and top-down processes. We measured theta responses elicited by a fast stimulus train inducing apparent motion. During the *ambiguous* task the perceived motion direction switched between horizontal and vertical motion or vice versa, even though the physical properties of the presentation did not. During the *unambiguous* task a switch in perception was externally triggered by a slight reconfiguration of the stimulus (see Fig. 1A and B and for animations also Supplementary Figs. 1–3). The stimulus onsets of the ongoing-presented stimulus train were used to select time periods of perceptual *switching* and *non-switching* for both tasks (see Fig. 2 and *Methods* section for detailed explanation).

Perceptual-motor requirements were comparable for both tasks (*ambiguous* and *unambiguous*). This is important since frontal brain activity may be related to the button press reporting a perceptual switch (Frässle et al., 2014). To further control for influences of the motor response on theta oscillations, a *motor control* task was included in the study design (Cruikshank et al., 2012). During this task participants were instructed to press a button randomly at their own, self-chosen pace.

Given previous reports, we expected that transient changes of the neuronal response related to perceptual *switching* would be reflected by an increase of theta activity. This increase was expected during

both the *ambiguous* and *unambiguous* tasks. We further assumed that the ongoing theta activity would differ between the *ambiguous* and *unambiguous* tasks since the specificity of the incoming sensory information would be constantly reduced for the *ambiguous* stimulus. The above reviewed studies demonstrate the prominence of anterior theta activity specifically during cognitive demands (e.g. Schmiedt-Fehr and Basar-Eroglu, 2011). Accordingly, we hypothesised that during the *ambiguous* task the anterior-posterior gradient of theta activity would be steeper than during the *unambiguous* task (see Fig. 1C for a schematic sketch of the expected results).

2. Methods

2.1. Participants

Twelve right-handed volunteers (nine women) between 20 and 31 years (mean age: 23.2, SD: 3.5) gave written consent for their participation, had normal or corrected-to-normal vision and reported to be free from neurological or psychiatric diseases.

2.2. Stimuli and tasks

Fig. 1A depicts the stimuli presented to elicit apparent motion perception. The main rationale of the study design was that perceptuo-motor requirements should be comparable between the *ambiguous* and *unambiguous* tasks: Each perceptual switch during the *ambiguous* task, that is a switch in perceived motion direction, had to be initiated by an event in the ongoing stimulus train to match the *unambiguous* task (see below as well as Supplementary Fig. 1 for a detailed explanation). Utilisation of the apparent motion paradigm further ensured comparable visual stimulation between *switching* and *non-switching* time periods. A *motor control* task allowed estimating for influences of motor potentials on the electrophysiological response during perceptual *switching*.

2.2.1. Ambiguous task

The Stroboscopic Alternative Motion stimulus (SAM) was presented during the *ambiguous* task. Alternating two stimuli, comprising two dots, generates the SAM (Kruse et al., 1986). For stimulus *Amb1* the dots are displayed on the top left and bottom right and for stimulus *Amb2* on the top right and bottom left (see Fig. 1A). As indicated by its name, the SAM combines two aspects of visual illusions: (1) The display of dots in alternation with other spatially shifted dots induces illusory stroboscopic motion, that is, the illusion that dots move from one position to the other. The onset of a new display, thereby, terminates the current and initiates the new motion perception. (2) The diagonal organisation of the double-dot-displays renders the SAM *ambiguous*: The perceived motion direction might be either horizontal or vertical. During continuous viewing this attribution may be maintained or switched (Kruse et al., 1986). Both, *switching* and *non-switching* time periods may, therefore, be compared time-locked to separate onsets of the double-dot-displays (see below for the precise procedure to time-lock *switching* and *non-switching* time periods).

2.2.2. Unambiguous task

For the *unambiguous* task a slightly modified stimulus allowed directional changes to be applied exogenously. The *unambiguous* vertical motion stimulus was generated by an alternating presentation of both dots either at the bottom or the top of the display (see Fig. 1A, *Vert1* and *Vert2*). The *unambiguous* horizontal motion stimulus was generated by an alternating presentation of both dots either at the left or the right side of the display (see Fig. 1A, *Horz1* and *Horz2*). Presentation of vertical or horizontal motion was switched exogenously, that is an exogenously induced switch in perceived motion direction started with each stimulus onset first replacing vertical motion stimuli with horizontal motion stimuli or vice versa. The reversal rate (measured in reversals

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