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Attentional modulations of somatosensory alpha, beta and gamma oscillations dissociate between anticipation and stimulus processing

Freek van Ede, Szabolcs Szebényi, Eric Maris *

Radboud University Nijmegen, Donders Institute for Brain, Cognition and Behaviour, The Netherlands

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ABSTRACT

What are the spectral signatures of somatosensory attention? Here we show that the answer to this question depends critically on the sensory context in which attention is deployed. We recorded magnetoencephalography (MEG) in humans and investigated tactile spatial attention in two different sensory contexts: in anticipation and during the processing of sustained tactile stimuli. We observe a double dissociation between these contexts and two key electrophysiological correlates of attention: in anticipation we primarily observe an attentional suppression of contralateral alpha and beta oscillations (8–12 and 15–30 Hz, respectively), whereas during stimulus processing we primarily observe an attentional amplification of contralateral gamma oscillations (55–75 Hz). This dissociation is well explained by the different neural states that occur prior and during the stimulus, and on which attention can exert its influence. In line with analogous observations in the visual modality, this suggests that the neural implementation of attention must be understood in relation to context and existing brain states. Consequently, different signatures of attention may contribute to perception in different contexts and, as our data reveals for the attentional modulation of alpha oscillations, these are not always required for attention to improve perception. At the same time, these data demonstrate that the attentional modulations of alpha and gamma oscillations (during, respectively, attentional orienting and attentional selection), are generalizable phenomena across the different sensory modalities.

Introduction

A major challenge in cognitive and systems neuroscience is to understand the neural mechanisms via which attention allows the selective processing of one aspect of the environment while ignoring others (Desimone and Duncan, 1995). To date, studies into the neural mechanisms of attention have revealed multiple neural correlates. For example, in regions of sensory cortex that process the task-relevant stimulus, attention has been shown to increase firing rate (Luck et al., 1997), blood flow (Kastner et al., 1999) and gamma oscillations (Fries et al., 2008), and decrease spike-rate (noise) correlations (Cohen and Maunsell, 2009) and alpha and beta oscillations (Foxe et al., 1998; van Ede et al., 2011; Worden et al., 2000). A key question that emerges is whether these different correlates are merely different reflections of the same underlying processes (and thus collectively *constitute* attention) or, rather, whether they relate to distinct components of attention and therefore might dissociate between experimental conditions. Here we addressed this question with regard to two of the aforementioned electrophysiological correlates of spatial attention: (1) the suppression of oscillations in the alpha and the beta band, and (2) the amplification of oscillations in the gamma band.

Although both these correlates have been well-established over the past 15 years, careful inspection of the literature reveals an important distinction. The attentional modulation of alpha oscillations in the visual modality (Foxe et al., 1998; Kelly et al., 2006; Thut et al., 2006; Worden et al., 2000; Wyart and Tallon-Baudry, 2008) and alpha and beta oscillations in the somatosensory modality (Haegens et al., 2011; Jones et al., 2010; van Ede et al., 2010, 2011, 2012a, 2012b) is typically reported in studies that investigate attention in the interval between a symbolic spatial cue and an anticipated target (i.e. in anticipation). In contrast, the attentional amplification of gamma oscillations is almost exclusively reported in studies in which attention is directed to a sustained stimulus (i.e. during stimulus processing; Fries et al., 2008; Gregoriou et al., 2009; Siegel et al., 2008). Thus, while both correlates are well-established, an important issue pertains to whether these different correlates co-occur or, alternatively, are unique to the specific sensory context in which attention is investigated (i.e. before or during the stimulus). Interestingly, several previous studies in the visual modality have already investigated this issue and have proposed that the attentional modulation of alpha oscillations is mainly related to the *orienting* of attention, whereas the attentional modulation of gamma oscillations is mainly related to the attentional *selection* of sensory information

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* Corresponding author at: Radboud University Nijmegen, Donders Institute for Brain, Cognition and Behaviour; Montessorilaan 3, 6525 HR Nijmegen, P.O. Box 9104, 6500 HE Nijmegen, The Netherlands. Fax: +31 243616066.

E-mail address: e.maris@donders.ru.nl (E. Maris).

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(Fan et al., 2007; Siegel et al., 2008; Wyart and Tallon-Baudry, 2008). Here we investigated whether this generalizes to the somatosensory modality.

If the neural correlates of attention are context-dependent, then this has several implications. First, it would suggest that the neural implementation of attention cannot be understood in relation to a fixed set of its correlates. Instead, it might be better understood as a mechanism that operates on existing patterns of neural activity (rather than a mechanism that instantiates these patterns). We provide direct evidence for this: corresponding to the stimulus-induced change in the oscillatory state, we observe that attention primarily suppresses contralateral alpha and beta power in anticipation, while it primarily amplifies contralateral gamma power during stimulus processing. Second, the context-dependence of neural correlates of attention would restrict the behavioral relevance of the different correlates of attention to specific sensory contexts. In fact, we report a large attentional improvement in perception without any concurrent attentional alpha modulation during sustained stimulus processing. This reveals that this specific spectral signature (as recorded with MEG) is not always required for attention to improve perception.

Materials and methods

Participants

18 subjects (12 male; age-range: 22–50 years) participated in the experiment. One participant was excluded due to chance level performance, another due to an incomplete understanding of our instructions as a result of a language barrier. The experiment was conducted in accordance with guidelines of the local ethical committee (Committee on Research Involving Human Subjects, Region Arnhem-Nijmegen, The Netherlands).

Tactile stimulation

For tactile stimulation, we used piezoelectric Braille cells (Metec, Stuttgart, Germany). A single Braille cell consists of eight pins (pin diameter: 1.5 mm; inter-pin spacing: 2.5 mm), aligned in two series of four (Fig. 1), that can be raised and lowered. When raised, these pins stand 1 mm out of their casing. Five such cells, together with a response button at the location of the thumb, were built in to a graspable device (for a graphical depiction, see van Ede et al., 2010; Fig. 1A). We used two such devices, one for each hand.

Tactile stimulation always occurred on both hands (all fingers, excluding the thumbs), at a rate of 50 Hz. Stimuli contained two features (a proximity and a motion feature; Fig. 1), each having two levels (proximal/distal and leftward/rightward, respectively). For each trial we randomly drew these levels independently per feature and per hand. The proximity feature involved a higher percentage of pins presented to either the proximal or distal part of the fingertips. For example, at every 50 Hz cycle of a *distal* stimulus, each of the four distal pins would have a probability of 0.12 to be presented versus a probability of 0.01 for each of the four proximal pins. For the motion feature, one finger per hand received a stronger stimulus ($p = 0.85$ for all pins) and this stimulus jumped left- or rightward across the fingers within a hand every 300 ms (3.3 Hz/finger, or, equivalently, every 15 beats of the 50 Hz stimulus). This induced a sensation of sweeping motion. Following a practice session we adjusted the above probabilities (for both the proximity and the motion tasks) slightly in several participants.

Task & procedure

We employed a cued tactile identification task (Fig. 1). Each trial started with a 300 ms visual cue. A word (“motion”/“proximity”/“ignore”; Fig. 1) instructed subjects to identify the proximity or the motion feature of the stimulus (attend trials), or to ignore this stimulus (ignore trials). In the attend trials, this instruction was paired with an arrow pointing to the left or right, indicating the hand for which the identity of the tactile stimulus should be evaluated (the attended hand). Following cue-onset, there was a 2.5 s anticipation interval followed by a 2.5 s stimulation interval (shaded intervals in Fig. 1). A response screen followed 500 ms after stimulation. In 10% of the attend trials, prior to the response screen, subjects were asked about the identity of the stimulus on the unattended hand (invalid trials). In proximity trials, subjects pressed the left (right) button to indicate a proximal (distal) stimulus; in motion trials, they pressed the left (right) button to indicate a leftward (rightward) moving stimulus. Buttons were pressed with the left and right thumbs. Confidence was indicated by a bar that filled up as long as the button remained pressed. In ignore trials, subjects could ignore the stimulus patterns and were only required to bring the confidence bar to a predetermined location, indicated by a line on the screen. As feedback, the fixation-cross turned red (incorrect) or green (correct) for 200 ms. Inter-trial-intervals were between 1 and 2.5 s. Trial types occurred with equal probability and were randomly intermixed. In 2 sessions of an hour, subjects completed around 700 trials.

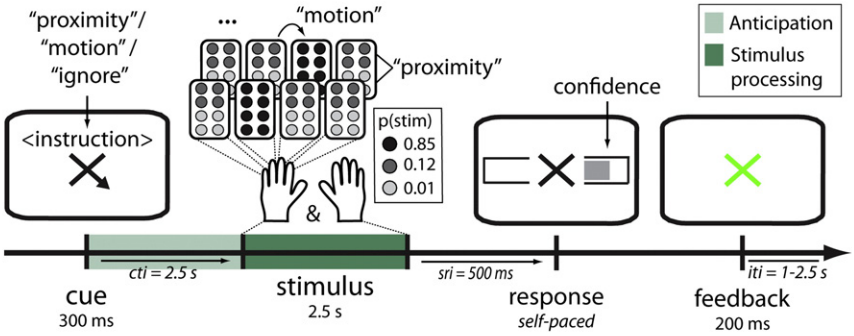

Fig. 1. Cued tactile identification task. Each trial started with a 300 ms visual cue. A word instructed subjects to identify the “proximity” or the “motion” feature of the stimulus (attend trials), or to “ignore” this stimulus (ignore trials). In attend trials, this instruction was paired with an arrow pointing to the left or right, indicating the hand for which the identity of the tactile stimulus should be evaluated. Following cue-onset, there was a 2.5 s anticipation interval (light green shading) followed by a 2.5 s stimulation interval (dark green shading). Stimuli were always presented to both hands and contained both a proximity and a motion feature (that was independent between the hands). In proximity trial, subjects were required to identify whether at the cued hand the stimulus was on average more proximal or distal. In motion trials, subjects were required to identify whether at the cued hand the stimulus contained a leftward or a rightward motion (see Materials and methods section for details). In 10% of the attend trials, at the end of the stimulus period, subjects were instructed to report the pattern of the cued feature on the uncued hand (invalid trials). 500 ms after stimulation, a response screen was presented. In proximity trials subjects pressed the left (right) button to indicate a proximal (distal) stimulus; in motion trials subjects pressed the left (right) button to indicate a leftward (rightward) moving stimulus. Confidence was indicated by a bar that filled up as long as the button remained pressed. A change in color of the fixation cross served as feedback. In ignore trials, subjects could ignore the stimulus patterns and were required to bring the confidence bar to a predetermined location, indicated by a line on the screen. *cti*, cue target interval; *sri*, stimulus–response-screen interval; *iti*, inter trial interval.