Preparatory alpha-band oscillations reflect spatial gating independently of predictions regarding target identity

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Abstract

Preparatory modulations of cortical alpha-band oscillations are a reliable index of the voluntary allocation of covert spatial attention. It is currently unclear whether attentional cues containing information about a target’s identity (such as its visual orientation), in addition to its location, might additionally shape preparatory alpha modulations. Here, we explore this question by directly comparing spatial and feature-based attention in the same visual detection task while recording brain activity using magneto-encephalography (MEG). At the behavioural level, preparatory feature-based and spatial attention cues both improved performance, and did so independently of each other. Using MEG, we replicated robust alpha lateralisation following spatial cues: in preparation for a visual target, alpha power decreased contralaterally, and increased ipsilaterally to the attended location. Critically, however, preparatory alpha lateralisation was not significantly modulated by predictions regarding target identity, as carried via the behaviourally effective feature-based attention cues. Furthermore, non-lateralised alpha power during the cue-target interval did not differentiate between uninformative cues and cues carrying feature-based predictions either. Based on these results we propose that preparatory alpha modulations play a role in the gating of information between spatially segregated cortical regions, and are therefore particularly well suited for spatial gating of information.

Keywords: spatial attention, feature-based attention, magnetoencephalography, alpha lateralisation, identity prediction

New & Noteworthy

The present work clarifies if and how human brain oscillations in the alpha-band support multiple types of anticipatory attention. Using magnetoencephalography, we show that posterior alpha-band oscillations are modulated by predictions regarding the spatial location of an upcoming visual target, but not by feature-based predictions regarding its identity, despite robust behavioural benefits. This provides novel insights into the functional role of preparatory alpha mechanisms and suggests a limited specificity with which they may operate.
Introduction

When expecting a task-relevant stimulus, we often have multiple types of predictive information, for example about its spatial location as well as its identity. In such cases, we can optimise behaviour using both space- and feature-based attention (Egner et al., 2008; White et al., 2015). In this study, we investigate whether and how oscillatory rhythms in the alpha-band reflect multiple types of anticipatory attention signals.

The role of alpha-band (8-14Hz) oscillations in spatial attention has been an active area of research for over a decade. In preparation for an upcoming visual target, attention to a particular location decreases posterior alpha power contralaterally to the attended location and increases alpha power ipsilaterally to the attended location (Worden et al., 2000; Sauseng et al., 2005; Kelly et al., 2006; Thut et al., 2006; Siegel et al., 2008). Similar alpha lateralisation with attentional allocation is also observed in the somatosensory system when anticipating tactile stimuli (van Ede et al., 2011; Haegens et al., 2011a). Such preparatory alpha modulations have been proposed to reflect functional inhibition of sensory regions processing irrelevant information and/or a release of inhibition of those regions processing relevant information (Jensen and Mazaheri, 2010; Foxe and Snyder, 2011; Jensen et al., 2012; Klimesch, 2012). Critically, these alpha modulations have been shown to be functionally relevant, predicting task performance on a trial-by-trial basis (Hanslmayr et al., 2007; van Dijk et al., 2008; Mathewson et al., 2009; Romei et al., 2010).

Despite the wealth of literature on alpha oscillation in preparatory spatial attention, it is currently not clear whether alpha lateralisation is modulated by content predictions in addition to spatial predictions. Content predictions can be hypothesized to influence preparatory alpha modulations in at least two ways. First, content predictions may strengthen alpha modulations. The opportunity to preload the anticipated target identity into working memory might lead to stronger engagement in relevant (contralateral) visual areas. Conversely, identity predictions could also be hypothesized to lead to weaker alpha modulations, as only those populations coding for the expected target features need to upregulate their excitability (as putatively indexed by the alpha modulation), as opposed to the larger cortical population coding for all possible target identities.

Here, we independently manipulated spatial and feature-based preparatory attention, while recording brain activity using magneto-encephalography (MEG). In contrast to our hypotheses, target-identity predictions did not significantly modulate alpha oscillations, despite having a clear benefit on performance. We propose that alpha power that can be detected at the spatial scales accessible to MEG does not show significant modulations when task-relevant feature levels compete for representations within brain regions.
Methods

Participants

All experimental protocols were reviewed and approved by the Central University Research Ethics Committee of the University of Oxford. Twenty volunteers took part in the experiment (9 male, 18 – 35 years, all right-handed). All participants had normal or corrected-to-normal vision and were naïve to the purpose of the experiment. Participants gave written informed consent before taking part, and received financial compensation (£15/hour for sessions involving MEG and £10/hour for sessions involving only behavioural testing).

Procedures

In order to examine the role of brain rhythms in preparatory feature-based and spatial attention, we asked participants to perform a target-detection task on two peripheral orientation stimuli, which were preceded by a cue. Figure 1 provides a task schematic of the experimental task. Participants completed two experimental sessions on separate days. An initial behavioural session was conducted to provide training on the behavioural task. Task performance was accompanied by MEG recordings in a second session, always completed within one week from the training session.
**Figure 1.** A. Trial procedure. B. Examples of the cues used in the different cueing conditions. Here, the parts of the cue highlighted in blue indicate the relevant feature dimension and/or spatial location while the background colour is magenta. Highlight and background colour were counterbalanced between participants. Feature and spatial cueing were independently manipulated resulting in four conditions: neutral cues (N), feature-only cues (F), spatial-only cues (S), and combined spatial-feature cues (SF). C. Behavioural results in the MEG session. Valid spatial cueing led to shorter RTs (in ms) and higher accuracy. Valid feature cueing shortened RTs and improved accuracy. Feature and spatial cueing did not interact. Error bars reflect ±1 standard error of the mean.

**Task and Stimuli**

The task was programmed in MATLAB v.7.10 (MathWorks) and presented using the Psychophysics Toolbox in Matlab (Kleiner et al., 2007). Stimuli were back-projected (Panasonic PT D7700E) onto a screen at a viewing distance of 120 cm with a spatial resolution of 1280 by 1024 pixels and a refresh rate of 60 Hz. Stimuli appeared against a uniform mid-grey background.

The task involved detecting the presence of a target orientation stimulus (horizontal or vertical grating) within an array of two peripherally presented gratings (left and right visual field). Arrays were preceded by a centrally presented attentional cue that could contain information regarding the target’s location (left/right), its identity (vertical/horizontal), or both (see Figure 1B). Spatial and feature cueing was thus independently manipulated resulting in four different conditions: neutral cueing (N), spatial-only cueing (S), feature-only cueing (F), and combined spatial-feature cueing (SF). A target stimulus was present in 50% of trials. When the target was present, a distracting tilted-orientation grating stimulus (45 degrees) occurred on the other visual field. Target-absent arrays always contained two tilted gratings. These could have the same or different orientations. Participants were instructed to maintain central fixation during task performance.

Trials began with a 1,000 – 1,500 ms (randomly determined) presentation of a central fixation dot (0.1° visual angle in width and height). This was followed by the presentation of a central cue stimulus for 200 ms. The cue stimulus consisted of a diamond shape (1.6° visual angle in width and height) around a plus-sign in its centre. To cue spatial location (left versus right) the left or right half of the diamond shape was highlighted in blue or magenta. To cue the feature identity (horizontal versus vertical) the vertical or horizontal line of the plus sign was highlighted in blue or magenta (see Figure 1B). The highlighting colour was counterbalanced between participants, with the other colour serving as the default ‘background’ colour of the cue stimulus (i.e. the neutral cue was either all blue or all magenta). Participants were explicitly told that cues did not predict whether the target would be present or absent, but that, instead, if the target would be present, it would occur at the cued location, and be of the cued identity (if this information was contained in the cue).

Following a cue-target inter-stimulus interval (ISI) of 1,200 ms, a stimulus array was presented for 50 ms, and then backwards-masked (after an interval of 67 ms) for 283 ms. Stimulus arrays consisted of either a horizontally or vertically oriented target Gabor patch (Gaussian-vignetted sinusoidal gratings) and a ±45° tilted distracter Gabor patch (target present), or two distracter tilted Gabor patches (target absent). Gabor patch stimuli (diameter: 2° of visual angle) were presented at a contrast for which the target detection task was performed at 75% accuracy (see below for details of the Staircasing procedure) with a spatial frequency of 3 cycles per degree. The Gaussian envelope had a space constant of 0.44°. The orientations of the target and distracter stimuli were pseudo-randomly selected on each trial. A target was present on half the trials (randomly selected at the beginning of the experiment).
Gabor patches were presented ±5.2° from the vertical meridian and 3° below the horizontal meridian. Backwards-mask stimuli were constructed by applying a Gaussian-vignette to the convolution of 100% contrast square-wave gratings at four orientations of 90°, 180°, 45°, and -45° angle. Stimuli and masks were presented atop 10% contrast luminance pedestals, which were present throughout the entire experiment. Participants responded (target present or absent) by making a right-handed index or middle finger button press during a response period of up to 2,000 ms. Response mappings were counterbalanced between participants. The subsequent inter-trial interval (ITI) was 1,000 ms (±500 ms). All conditions were equiprobable and randomized.

Participants performed a calibration session before the behavioural training and MEG experimental session using an adaptive psychophysical staircase procedure to estimate the threshold contrast for perceiving the Gabors. Task difficulty was adjusted for each participant by titrating the contrast of the Gabor patches for which the target detection task was performed at 75% accuracy when only neutral cues were used.

**Behavioural training session**

Prior to the MEG session, on a separate day, participants were trained on the behavioural task to ensure they were familiar with the task and could efficiently use the different cue types. Participants completed a total of 288 trials of the experimental task (split into three runs) in a MEG mock scanner. In each run, short rest periods were introduced every 32 trials. The first run served as a practice run to familiarise participants with the task, and stimulus contrast was set to 50%. All cues were included in this run. The second run comprised the staircase procedure starting at 50% contrast, and was repeated if necessary. Only neutral cues were included in the staircase run. In the third run, the contrast was set to the threshold estimated from the staircase, and spatial, feature, and spatial-feature (but no neutral) cues were included.

**MEG session**

Whole-head MEG recordings were acquired with a 306-channel Vectorview system (Elekta-Neuromag, Helsinki, Finland) at the Oxford Centre for Human Brain Activity (OHBA). The system contains 306 sensors: 102 magnetometers and 204 orthogonally oriented planar gradiometers (102 latitudinal gradiometers, 102 longitudinal gradiometers). The MEG scanner was housed in a three-layer magnetically shielded room (ImedcoAG). The data were sampled at 1000 Hz.

Additional electrodes were used to record eye movements (EOG) and heart rate (ECG) during MEG acquisition. A vertical pair of EOG electrodes was placed above and below the left eye to detect blinks. To detect lateral eye movements, a horizontal pair was placed with one electrode to the left of the left orbit, and the other electrode to the right of the right orbit. Electrodes were placed on the left and right wrist to record ECG. In addition, eye movements were monitored online and recorded at 1,000 Hz with a remote infrared eye-tracker (SR research, EyeLink 1000) controlled via the Psychophysical Toolbox in Matlab v.7.10 (MathWorks). Four magnetic coils served as head-position indicator (HPI) coils. These were positioned on each mastoid bone and on each side of the forehead near the hairline. The positions of the HPI coils relative to 3 fiducial points, as well as the subject's head shape, were digitized using a Polhemus 3D tracking system (Polhemus, EastTrach
3D). HPI coils were activated at the beginning of each block to localize the participant’s head with respect to the sensor array and to monitor the subject’s head position to correct for any head movements later during analysis.

During the recording session, participants sat in a reclining chair and supported their head against the back and top of the MEG helmet. Participants were asked to remain as still as possible during the recording session and were continuously monitored by a video camera. Participants were given a fibre-optic button box and made responses using their right and left index finger. Stimuli were projected onto a screen placed around 120 cm in front of the subject. MEG data were recorded in 5 blocks. Participants completed a total of 640 trials of the experimental task split into five blocks of 128 trials each. The four experimental conditions (SF, S, F, N) were presented in randomized order, resulting in a total of 160 trials per condition.

### Analysis

#### Behavioural Analysis

Hypotheses regarding the effects of experimental parameters on recall accuracy and reaction times (RTs, in milliseconds) in correct trials were tested using analysis of variance (ANOVA) and t tests (Bonferroni corrected where appropriate). To guide our interpretation of the MEG results, we only used participants’ performance during the MEG session.

#### MEG analysis

Analysis of the MEG data was performed using a combination of custom-written MATLAB scripts, in-house OHBA software library (OSL), SPM8 (Litvak et al., 2011); http://www.fil.ion.ucl.ac.uk/spm), and FieldTrip (Oostenveld et al., 2010); http://www.ru.nl/fcdonders/fieldtrip/). All time samples were corrected with respect to the refresh delay of the projector (measured on-line with a photodiode). MEG analysis was performed in two main steps: 1) preprocessing of the data to remove artefacts present in the raw data and 2) sensor-level analysis consisting of the time-frequency decomposition of the MEG data to examine the time-frequency dynamics of preparatory alpha-band modulations. The epoch of interest for analyses was the period between cue and target onset.

#### Preprocessing

The raw MEG data were visually inspected to remove any channels with excessive noise. The data were then de-noised using Maxfilter signal-space separation (Taulu et al., 2005), and compensated for changes in head position within-session using the MaxMove software, both implemented in MaxFilter version 2.2 (Elekta Neuromag). The MaxFilter software works by mathematically transforming the data to a set of virtual sensors, which is made possible by location information provided by the MEG sensor array and each person’s continuous head position signal recorded from the HPI coils. Transforming the data into virtual sensors gives a standard reference frame and allows for data to be combined across recordings. The data were subsequently down-sampled to 250 Hz. After applying a high-pass filter at 1 Hz, the data were then epoched with respect to each cue onset (from -2 s to + 3 s). This time-window encompassed both cue-target interval activity (from 0 s onward) and target-related activity (from 1.4 s onward). The resulting epochs were manually inspected for artefacts. Systematic artefacts (including eye blinks and heart beats) were identified and regressed out of the data using the following procedure.
Independent component analysis (ICA) was used to decompose the sensor data for each session into 150 temporally independent components (tICs) and associated sensor topographies using FastICA (http://research.ics.aalto.fi/ica/fastica). Artefact components were manually identified by the combined inspection of the spatial topography, time course, kurtosis of the time course and frequency spectrum for all components. Artefactual components were then rejected by subtracting them out of the data (in the majority of cases 3-5 components were removed from each subject). Finally, data were imported into Fieldtrip and inspected using the semi-automatic rejection tool to discard any remaining trials with excessive variance at 8 – 14 Hz.

**Time-frequency analysis**

Time-frequency analysis of the time-domain sensor-space signal was performed using a Fast Fourier transformation algorithm for the range of frequencies between 3 and 30 Hz. The interval -1 s to +2.5 s centred on cue onset was used for analysis. Data from within a 300-ms sliding time window, which was advanced in steps of 60 ms, was Fourier-transformed and multiplied with a Hanning taper in 1-Hz steps. As a result of the 300 ms sliding time window, all depicted time points incorporate signal from ± 150 ms around that time point. We then averaged the resulting power spectra over trials within each condition of interest. Magnetometers were discarded and the power time-series in the gradiometer pairs were combined (Cartesian sum, i.e. summing the squares of the latitudinal and longitudinal gradiometer activity and taking the square root) resulting in a 102 sensor combined planar gradiometer map of sensor space time-frequency power.

For each participant, we first contrasted the power spectra between left and right spatial (SF and S) cues in all MEG channels and expressed this as a percentage change (i.e. [(left – right) / (left+right)*100]). Second, to examine effects of feature information on cue-induced alpha lateralisation, we calculated lateralisation indices for spatial-only (S) cues and for spatial-feature (SF) cues separately and compared them. Concretely, for clusters consisting of left and right MEG channels, we calculated the normalized difference in power between trials in which the target were expected contralateral or ipsilateral to those channels, and also expressed this as a percentage change: [(contralateral - ipsilateral) / (contralateral + ipsilateral)]*100. We subsequently collapsed this contralateral vs. ipsilateral metric across left and right channel clusters. The lateralisation indices were calculated twice using different channel selections: first including all left and all right MEG channels, and second focusing on alpha power in visual areas by focusing on a subset of the most informative MEG channels, which we will refer to as visual channels. To identify visual channels, we selected channels above left and right visual areas by plotting the group-level grand average alpha lateralisation (from the analysis described above, i.e. averaged over all types of spatial cues) and manually selected the five left and right channels that showed the maximal response (power suppression contralateral and increase ipsilateral).

Next, to examine the effects of feature information on alpha lateralisation in more detail, we compared the timecourses of contralateral and ipsilateral responses following spatial-feature (SF) versus spatial-only (S) cues. In contrast to the analysis described above, this time, we completed the analysis on visual channels only.

Finally, to examine effects of feature cueing on non-lateralised alpha power we also contrasted power spectra in feature-only (F) cueing to neutral (N) cueing conditions. This analysis was done on all channels as well as on visual channels.

At the group level, we tested for significance using cluster-based permutation statistics (5000 permutations, alpha-level .05), which circumvent the multiple
comparisons problem by evaluating the full dataspace under a single permutation distribution of the largest cluster (Maris and Oostenveld, 2007). Unless noted otherwise, clustering was performance across space (channels) and time (0 s to 1.4 s from cue onset), with regard to data that were averaged in the a-priori defined frequency band of interest (i.e. the alpha-band; 8 – 14 Hz).
Results

Behavioral Results
Repeated-measures analyses of variance (ANOVAs) were carried out on accuracy and RTs (RTs from correct trials only) with the factors spatial cue (present, absent) and feature cue (present, absent). Behavioural data are depicted in Figure 1. Significant main effects of spatial cueing were observed on RTs ($F(1,19) = 29.562$, $p < .001$, $\eta^2_p = 0.609$) as well as on accuracy ($F(1,19) = 24.548$, $p < .001$, $\eta^2_p = 0.564$). Target detection was more accurate and more efficient when preceded by a valid (S, SF) as opposed to a neutral spatial cue (N, F). Significant main effects of feature cueing were also observed on RTs ($F(1,19) = 22.902$, $p < .001$, $\eta^2_p = 0.547$) and accuracy ($F(1,19) = 4.913$, $p < .05$, $\eta^2_p = 0.206$), reflecting improved performance when information was given on the target’s identity (i.e. orientation). No significant interactions were observed (RTs: $F(1,19) = 2.230$, $p = 0.152$; accuracy: $F(1,19) = 1.296$, $p = 0.269$).

To assess whether feature information alone improved performance we compared feature-only to neutral cues, and spatial-feature to spatial-only cues using repeated-measures t-tests. RTs were shortened ($t(19) = 4.99$, $p = .001$, $d = 1.12$) and accuracy improved ($t(19) = 2.33$, $p = .031$, $d = 0.52$) for feature-only cues compared to neutral cues. Similarly, RTs were shortened ($t(19) = 3.71$, $p = .002$, $d = 0.83$) for spatial-feature compared to spatial-only cues while there was no significant effect on accuracy ($t(19) = 1.16$, $p = .261$, ns).

MEG Results
Modulations of posterior alpha-band lateralisation by spatial and feature cueing
To assess the spatial cueing effect, we compared alpha-band power following left versus right spatial cues (S, SF). To this end, we compared alpha power (averaged over 8 – 14 Hz) from 0 s to 1.4 s post cue onset, between left and right spatial cues. A cluster permutation test on this contrast in the alpha-band (8 – 14 Hz), considering all time points from 0 s to 1.4 s and all MEG channels, revealed a significant positive cluster over left posterior sensors from 0.32 s to 1.3 s ($p = .0044$) and a just-significant negative cluster over right posterior sensors from 0.44 s to 0.92 s after cue onset ($p = .0452$). Figure 2A depicts this contrast, averaged over all significant time points of the positive cluster. Next, we calculated alpha lateralisation indices, combining left and right cues to calculate contralateral and ipsilateral preparatory activity, and then contrasting the two (see Figure 2B). To assess how alpha lateralisation following spatial cues was modulated by the presence of feature information, we calculated the alpha lateralisation indices separately for spatial-feature (SF) and spatial-only cues (S), first using all left and right MEG channels and then using a subset of the left and right visual channels (Methods for details) only. Figure 2C depicts the time courses of the alpha lateralisation indices for the two conditions using all channels, and Figure 2D shows the same using visual channels only. A comparison of the alpha lateralisation indices over all channels (considering all time points and frequencies between 3 – 30 Hz) revealed one significant positive cluster (4 Hz to 16 Hz, 0.44 s to 0.62 s, $p = .025$), showing a stronger (possibly faster) lateralisation when the cue contained no feature information, in the spatial-only cueing condition (S). Similarly, this was the case when comparing alpha lateralisation indices over visual channels only (1 positive cluster, 6 Hz to 16 Hz, 0.32 s to 0.62 s, $p = .004$).
It is conceivable that this difference reflects differences in the demands to interpret the cue stimulus. It may be more straightforward to interpret S cues compared to SF cues, leading to a faster deployment of spatial attention with S compared to SF cues. Indeed, and critically, in the most relevant preparatory period just before the anticipated target onset (at 1.4s), the modulations by spatial attention were virtually indistinguishable between spatial-feature and spatial-only cues (i.e. spatial cues with and without target identity predictions). This was the case no matter what channel selection we used.

Figure 2. A. Topographic plots showing normalized difference in alpha power (8 – 14 Hz, averaged over significant time window) between left and right spatial cues, expressed as percentage change (i.e., ([left - right] / [left + right]) * 100). B. Average time-frequency representations of alpha lateralisation index (i.e. [(Contralateral - ipsilateral) / (contralateral + ipsilateral)]*100), calculated across all spatial cueing types (S, SF), collapsed over all channels, and time-locked to cue-onset. C and D. Time courses of alpha power lateralisation index for spatial-feature (SF, in blue) and spatial-only (S, in green) cues, averaged over all channels (C) and over visual channels (D), time-locked to cue-onset. The black bars denotes where the conditions are significantly different (cluster p < .05).

Contralateral and ipsilateral alpha-band responses relative to neutral cues
To evaluate alpha lateralisation more carefully we then looked separately at contralateral and ipsilateral alpha-band power changes in visual channels. To this end, we overlaid the time courses of spatial-only, combined spatial-feature, and neutral cues, normalized by a pre-cue baseline. As suggested by Figure 3, the
attentional modulation (vs. neutral) appeared slightly delayed for combined spatial-feature compared to spatial-only cues in both contra- and ipsilateral visual channels. Indeed, cluster-permutation tests, averaging over alpha-band power and visual channels, revealed a significant difference between ipsilateral responses following spatial-feature versus spatial-only cues (1 negative cluster from 0.38 to 0.68 s, p = .006, see Figure 3B). However, there was no difference between contralateral responses following spatial-feature versus spatial-only cues (see Figure 3A). Again, in both contra- and ipsilateral channels, these conditions became virtually indistinguishable toward the end of the cue-target interval. We further noted that both spatial-feature and spatial-only cues elicited significant contralateral and ipsilateral responses compared to neutral cues (contra spatial-feature versus neutral: 1 negative cluster from 0.44 to 0.62 s, p = .024; contra spatial-only versus neutral: 1 negative cluster from 0.44 to 0.56 s, p = .047; ipsi spatial-feature versus neutral: 1 positive cluster from 0.86 to 1.4 s, p < .001; ipsi spatial-only versus neutral: 1 positive cluster from 0.44 to 1.4 s, p < .001; see Figure 3A and B).

Figure 3. Time courses of contralateral (A) and ipsilateral (B) alpha power responses, averaged over visual channels, for spatial-feature (blue line) and spatial-only (green line) cues, together with alpha power responses following neutral cues (black line), time-locked to cue-onset. The dotted and solid blue bars denote significant differences between neutral cueing and spatial-only cueing conditions and between neutral cueing and spatial-feature cueing conditions, respectively (p < .05).

Modulations of non-lateralised alpha-band power by feature cueing

As stated above, it is feasible that the observed difference in alpha lateralisation between spatial-feature and spatial-only cues from 0.44 s to 0.62 s after cue onset reflects low-level differences in cue processing (as spatial-feature cues are more complex than spatial-only cues). Alternatively, however, this initially reduced alpha lateralisation with feature information could also be due to a global modulation linked
to preparatory feature-based attention (Treue and Martínez Trujillo, 1999; McAdams and Maunsell, 2000; Saenz et al., 2002; Martinez-Trujillo and Treue, 2004; Bichot et al., 2005; Serences and Boynton, 2007; Jehee et al., 2011) whereby alpha power might be attenuated in a non-lateralised fashion (thereby potentially countering and/or delaying the lateralisation effect). If so, then one would expect such global modulation also to show in the contrast between pure feature (F) and neutral (N) cues. However, cluster permutation tests on the averaged alpha-band power (8 – 14 Hz), considering all time points from 0 s to 1.4 s and all channels (Figure 4A), or all visual channels (Figure 4B), revealed no significant clusters.

We also explored other frequency-bands across all channels and time points, but did not find any robust effects. Concretely, we compared power in the predefined theta (4 – 8 Hz), alpha (8 – 14 Hz), beta (14 – 30 Hz), and gamma (40 – 100 Hz) bands between feature-only and neutral cues. Cluster-based permutation tests, averaging over respective frequency bands and considering all time points from 0 s to 1.4 s and all MEG channels, only revealed one significant positive cluster in the theta band from 0.152 s to 0.508 s (p = .003) that centred on medial frontal channels (see Figure 5). While this is a potentially interesting effect, its relative early timing suggests that it too may reflect differences in cue processing, rather than a sustained effect of anticipatory attention. Moreover, this analysis was only exploratory and did not correct for multiple comparison across frequencies.

Figure 4. Time courses of alpha power averaged over all channels (A) or over visual channels only (B) for neutral cues (N, in black) and feature-only (F, in red) cues, time-locked to cue-onset. Conditions are not statistically different from one another.
Figure 5. Topographies showing uncorrected t-values (top) and cluster-corrected p-values (bottom) of the pure feature versus neutral contrast for theta (4 – 8 Hz), alpha (8 – 14 Hz), beta (14 – 30 Hz), and gamma (40 – 100 Hz) frequency bands throughout the cue-target interval in 200-ms intervals.

Discussion
In this study, we set out to investigate whether predictions about target identity, in addition to predictions about locations, modulate preparatory attentional alpha modulations. We considered two hypotheses: target identity predictions may strengthen alpha modulation due to relevant cortical areas showing stronger engagement (e.g. by loading the target template into working memory), or target identity predictions may lead to weaker alpha modulations as only selected populations coding for the expected target feature modulate their excitability (as opposed to the larger cortical population coding for all possible target identities). Our results do not provide support for either hypothesis. Preparing for the spatial location of an upcoming visual target stimulus elicited robust alpha lateralisation. However, when observers additionally held predictions about the identity of the upcoming target (and prepared both for the spatial location and the orientation of the upcoming
target), alpha lateralisation was not further modulated apart from an early difference that was likely related to delayed deployment of attention with more complex cues (i.e. there was no alpha modulation in the most relevant preparatory time window). Of course we cannot rule out that both hypothesised mechanisms were at play, counteracting one another (i.e. stronger engagement of a smaller population) but we consider it highly unlikely that this would result in a perfectly balanced activation pattern. It is key to note that the lack of an observed modulation of alpha lateralisation (as well as non-lateralised power) by feature-based attention was not due to the fact that the feature cues were not effective, because they did elicit a clear behavioural performance benefit. Similarly, it is important to highlight that neutral cues were effective at shifting attention as they provided useful information for preparation (Nobre and Rohenkohl, 2014; Posner, 1980), and only lack information about the most likely feature/location of the target.

Relation to other studies of feature-based attention and alpha oscillations
The role of alpha power in spatial attention has been studied extensively and several studies have demonstrated spatially specific modulations of alpha power in preparation for an upcoming target stimulus (e.g. Worden et al., 2000; Sauseng et al., 2005; Thut et al., 2006), in line with the findings reported here. Fewer studies have assessed the effects of feature-based attention and target identity predictions on alpha power. Snyder and Foxe (2010) examined whether alpha mechanisms are also involved in non-spatial preparatory attention using a feature-dimension cueing task where either colour or motion information was task-relevant in different trials. Alpha power modulations were observed bilaterally along the dorsal stream in motion area MT when motion was task-relevant, or along the ventral stream in colour area V4 when colour was task-relevant. This study seems similar to ours but there is a key difference between the experimental designs. In our task, participants were cued to attend to local feature identities (horizontal versus vertical), processed by overlapping neural populations, while Snyder and Foxe (2010) cued participants to attend to feature dimensions, processed by large, non-overlapping specialized visual modules, and no specific target identity was known in advance.

In another related study, Mayer and colleagues showed modulation of alpha power over task-relevant brain regions by stimulus identity predictions (Mayer et al., 2016). Participants viewed a letter sequence consisting of two parts: initially, letter identity was unknown and revealed over successive trials as letter visibility increased. Following that, letter visibility was lowered back down to subthreshold levels. Participants made subjective ratings to each stimulus in a sequence regarding its detectability and identity. This design allowed comparing alpha power preceding letters whose identity was unknown (in the first half of a sequence) to letters whose identity was known (in the second half of a sequence), under identical sensory input. It was found that pre-stimulus alpha power increased over left occipital areas when stimulus identity was known compared to when it was not. Source-space analysis of the effect identified a set of areas in left temporal cortex previously linked to top-down letter processing and supramodal representations of letters. This study seems remarkably similar to ours as here predictions were made regarding actual feature values as opposed to feature dimensions. However, we used simple orientation stimuli while (Mayer et al., 2016) used more complex letter stimuli processed in more high-level areas, a potentially important difference as discussed below.
In contrast to our findings, another recent MEG study (de Lange, Rahnev, Donner, and Lau (2013) reported an increase in preparatory alpha power over occipital areas when observers held expectations about the feature composition of an upcoming stimulus – in that case its motion direction – compared to when observers did not have expectations. The authors proposed that this increase in alpha power with expectation was driven by selective modulation of subpopulations of direction-selective cells, challenging our findings. It is possible that modulations in oscillatory activity differ as a function of predictions about motion direction vs. stimulus orientation. However, there are at least two additional relevant points to consider that might account for this apparent discrepancy with our findings. First, neutral and informative cues were not perceptually matched in the previous study, which might have driven differences in their sensory processing that are unrelated to preparatory neural dynamics. The authors acknowledged this possibility. Secondly, in our task the cue-related prediction was orthogonal to the decision required for task performance (as participants performed a detection task), whereas in de Lange et al. (2013) it was. When predictions are also informative about the decisions and responses required, they may influence additional neural populations.

Finally, another recent study by van Diepen, Miller, Mazaheri, and Geng (2016) examined the role of alpha activity in spatial and feature-based attention. Participants performed a forced-choice identification task to a letter, which appeared inside a target shape presented alongside a distracter shape. Spatial attention was manipulated using predictive cues while feature-based attention was manipulated by varying target-distracter similarity (target shapes were always red while distracter shapes could be presented in one of four possible colours ranging from red to yellow). The authors showed that even when spatial cues were uninformative, alpha lateralisation to target stimuli emerged in low-similarity distracter trials. Given that van Diepen et al. (2016) focused on target processing and manipulated feature-based attention by varying target-distracter similarity, their results do not directly inform our question of how target content predictions affect alpha modulations in preparation for an upcoming target, and it is difficult to relate their findings to our results and the literature discussed above.

Albeit in different ways, the findings by Mayer et al. (2016) and Snyder and Foxe (2010) have thus suggested parallels between the role of alpha mechanisms in selective spatial attention and feature-based attention. One proposal that could reconcile the findings of these two studies with ours is that alpha oscillations play a role in gating information between distant, non-overlapping neural populations. We elaborate on this below.

How specific can preparatory alpha modulations be employed?

The functional role underlying alpha power modulations has been proposed to be the gating of information flow via active inhibition of non-task relevant cortical areas (e.g. Klimesch et al., 2007; Jensen and Mazaheri, 2010), for example by modulating neuronal spike rates (Haegens et al., 2011b). However, this account leaves open the specificity with which this mechanism can operate. We speculate that alpha modulations are predominantly involved in the gating of information processed by large, non-overlapping sensory area – be it between different retinotopical locations or different cortical areas that are specialised for processing different visual features (e.g. dorsal versus ventral feature dimensions as in Snyder and Foxe, 2010) – but not in the specific gating of information at the level of particular features that are coded in neighbouring cortical columns). Importantly, this would mean that alpha
mechanisms may be able to support feature-based attention (and identity predictions) only in tasks where information gating occurs between distant cortical areas that are specialised for processing different feature dimensions, or relatively high-level feature representations. Fine-grained, overlapping areas coding for early-level feature values may not be targetable by alpha mechanisms.

A likely explanation for this is that (EEG measured) alpha modulations reflect an aggregate measure that occurs at a larger scale than (for example) orientation columns. This explanation can account for the differences between the findings reported here, and the findings reported by Snyder and Foxe (2010) despite the apparent similarity of these two studies. Concretely, we used specific orientations (vertical versus horizontal), which are represented in interdigitating populations. In contrast, Foxe and Snyder (2010) used non-identity-specific feature dimensions (colour versus motion), which are coded in distant, non-overlapping dorsal versus ventral regions. Similarly, Mayer et al. (2016) reported alpha modulations by identity predictions in relatively high-level cortical processing areas. In other words, the crucial distinction is not between feature-based versus space-based attention, but about what relevant populations are engaged in a task and alpha modulations cannot operate at a level of specificity such as microcolumns.

The findings of a recent study (Harvey et al., 2013) suggest that it may be possible to measure finer-grained differences in target-induced alpha with higher spatial resolution using electrocorticography (ECoG). (Harvey et al., 2013) recorded separate fMRI and ECoG data from occipital and parietal areas of an epileptic patient, while the patient viewed drifting checkerboard bars of varying orientations. BOLD responses were used to estimate population receptive fields (pRF) for each stimulus. V1 electrodes whose pRF surround was stimulated showed increased alpha power compared to electrodes whose pRF center was stimulated, and this pattern was observed between electrodes only 1 cm apart with partially-overlapping visual field representations. These findings show that stimulus-induced alpha modulations can be highly localised, with differences evident between nearby V1 locations.

**Neural mechanisms of preparatory feature-based attention**

Given that we observed a robust behavioural benefit following feature-only cues, this must be due to some neural processes. We focused on both global and lateralized modulations of alpha power, and did not observe any robust signature of preparatory feature-based attention. Going beyond our initial hypotheses, we also conducted exploratory analysis in other frequency bands, but these analyses also did not yield conclusive results. We may not have been able to look properly at some putative anticipatory modulatory mechanisms. Additionally, there may have been some exogenous feature-based priming (Theeuwes, 2013) given that our cues highlighted the same visual features as the target stimuli. What the neural substrates are of the reported performance benefit by preparatory feature-based cues, alike the ones used here, thus remains an important avenue for future investigations.


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Figure Captions:

Figure 1. A. Trial procedure. B. Examples of the cues used in the different cueing conditions. Here, the parts of the cue highlighted in blue indicate the relevant feature dimension and / or spatial location while the background colour is magenta. Highlight and background colour were counterbalanced between participants. Feature and spatial cueing were independently manipulated resulting in four conditions: neutral cues (N), feature-only cues (F), spatial-only cues (S), and combined spatial-feature cues (SF). C. Behavioural results in the MEG session. Valid spatial cueing led to shorter RTs (in ms) and higher accuracy. Valid feature cueing shortened RTs and improved accuracy. Feature and spatial cueing did not interact. Error bars reflect {plus minus} 1 standard error of the mean.

Figure 2. A. Topographic plots showing normalized difference in alpha power (8 - 14 Hz, averaged _ over significant time window) between left and right spatial cues, expressed as percentage change (i.e., ([left - right] / [left + right]) * 100). B. Average time-frequency representations of alpha lateralisation index (i.e. ([Contralateral - ipsilateral] / (contralateral + ipsilateral)]*100), calculated across all spatial cueing types (S, SF), collapsed over all channels, and time-locked to cue-onset. C and D. Time courses of alpha power lateralisation index for spatial-feature (SF, in blue) and spatial-only (S, in green) cues, averaged over all channels (C) and over visual channels (D), time-locked to cue-onset. The black bars denotes where the conditions are significantly different (cluster p < .05).

Figure 3. Time courses of contralateral (A) and ipsilateral (B) alpha power responses, averaged over visual channels, for spatial-feature (blue line) and spatial-only (green line) cues, together with alpha power responses following neutral cues (black line), time-locked to cue-onset. The dotted and solid blue bars denote significant differences between neutral cueing and spatial-only cueing conditions and between neutral cueing and spatial-feature cueing conditions, respectively (p < .05).

Figure 4. Time courses of alpha power averaged over all channels (A) or over visual channels only (B) for neutral cues (N, in black) and feature-only (F, in red) cues, time-locked to cue-onset. Conditions are not statistically different from one another.
Figure 5. Topographies showing uncorrected t-values (top) and cluster-corrected p-values (bottom) of the pure feature versus neutral contrast for theta (4 - 8 Hz), alpha (8 - 14 Hz), beta (14 - 30 Hz), and gamma (40 - 100 Hz) frequency bands throughout the cue-target interval in 200-ms intervals.
A  Task

1000 - 1500 ms  200 ms  1200 ms  50 ms  67 ms  200 ms  ~
Fixation  Cue  Blank  Stimuli  Blank  Mask  Response

B  Cue examples
neutral (N)  feature-only (F)
spatial-only (S)  combined (SF)

C  Behavioural results

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<tr>
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<th>Reaction Time (in ms)</th>
<th>Accuracy</th>
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<tbody>
<tr>
<td>SF F</td>
<td>750 800 900</td>
<td>0.8</td>
</tr>
<tr>
<td>S N</td>
<td>775 825 925</td>
<td>0.8</td>
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