Attentional selection of location and modality in vision and touch
modulates low-frequency activity in associated sensory cortices

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Abstract

Selective attention allows us to focus on particular sensory modalities and locations. Relatively little is known about how attention to a sensory modality may relate to selection of other features, such as spatial location, in terms of brain oscillations, although it has been proposed that low-frequency modulation (alpha- and beta-bands) may be key. Here we investigated how attention to space (left or right) and attention to modality (vision or touch) affect ongoing low-frequency oscillatory brain activity over human sensory cortex. Magnetoencephalography was recorded while participants performed a visual or tactile task. In different blocks touch or vision was task-relevant, while spatial attention was cued to the left or right on each trial. Attending to one or other modality suppressed alpha oscillations over the corresponding sensory cortex. Spatial attention led to reduced alpha oscillations over both sensorimotor and occipital cortex contralateral to the attended location in the cue-target interval, when either modality was task-relevant. Even modality-selective sensors also showed spatial-attention effects for both modalities. The visual and sensorimotor results were generally highly convergent, yet, while attention effects in occipital cortex were dominant in the alpha-band, in sensorimotor cortex these were also clearly present in the beta-band. These results extend previous findings that spatial attention can operate in a multimodal fashion and indicate that attention to space and modality both rely on similar mechanisms that modulate low-frequency oscillations.
Introduction

Numerous recent studies have revealed modulations of oscillatory synchrony as a potential mechanism for attentional selection in sensory cortex (Jensen et al., 2007; Womelsdorf and Fries, 2007). Most studies focused on the effects of spatial attention, including anticipatory effects that follow an attentional instruction or cue, in advance of the expected imperative stimuli. A common finding is that attention to a particular location in space suppresses low-frequency alpha-oscillations in the corresponding neural population, for instance contralateral visual cortex (Worden et al., 2000; Trenner et al., 2008; Haegens et al., 2011, Siegel et al. 2008). These modulations of alpha oscillations are thought to reflect a gating mechanism that determines the readiness of neural populations to process afferent input (Foxe and Snyder, 2011; Jensen and Mazaheri, 2010). Importantly, this alpha suppression mechanism emerges in advance of the anticipated stimulus to attend and it has been shown that it can predict subsequent sensory performance (Thut et al., 2006; Haegens et al., 2011) and may play a causal role in attentional modulation (Romei et al., 2010). Several studies have also found spatial attention effects in the beta-band (Bauer et al. 2006, Siegel et al. 2008) although the neurophysiological mechanisms and the functional role of beta-oscillations seem somewhat more complex (Gross et al. 2004, Donner et al. 2007, Ziegler et al. 2010)

Although most studies of selective attention consider a single sensory modality at a time, a growing literature has studied possible crossmodal links in spatial attention (Macaluso and Driver, 2005). Several studies with a variety of measures have indicated that when attention is directed to a particular location in one modality (e.g., touch), other modalities (e.g., vision) may be spatially affected in a corresponding manner, even when task-irrelevant (Spence and
Driver, 1998; Eimer and Driver, 2001; Kennett et al., 2001; Eimer et al., 2002; Talsma et al., 2010). However, relatively few studies have addressed how crossmodal spatial attention may influence oscillatory activity, such as the low-frequency alpha-suppression mentioned above (Foxe and Snyder, 2011).

Bauer et al. (2006) reported that spatially attended tactile stimuli can suppress stimulus-related low-frequency activity in occipital cortex, suggesting a possible crossmodal effect; while Banerjee et al. (2011) reported similar parieto-occipital spatial attention effects in an auditory task as for a visual task. Jones et al. (2010), Haegens et al. (2011) and Van Ede et al. (2011) reported low-frequency changes over sensorimotor cortex for spatial attention in unimodal tactile studies (with respect to the target stimulus).

Relatively few studies have investigated oscillatory mechanisms of attention to one modality versus another, as opposed to attention to one location versus another. Some have either focused on synchrony in a non-frequency-specific way (Steinmetz et al., 2000), or with an emphasis on phase-modulations in the low-frequency theta band (Lakatos et al., 2008). Foxe et al. (1998) and Fu et al. (2001) investigated the impact of attention to modality on alpha-oscillations, but only for occipital alpha-oscillations in visuo-auditory tasks (Foxe and Snyder, 2011). We are unaware of any study to date that has investigated the impact of modality selection on neural oscillatory activity for more than one modality (e.g., not just for visual cortex when attending to a different modality, but also for the latter modality when attending vision). Furthermore, we are not aware of any oscillatory studies that have as yet examined the impacts of both spatial attention and of attention to a modality, as we investigated here in a visual-tactile task.
We used magnetoencephalography (MEG) to assess low-frequency oscillations in relation to spatial attention and modality attention in a visuo-tactile oddball task. Participants had to attend to one of two modalities (vision or touch), with the currently task-relevant modality being blocked in a counterbalanced manner, whereas the relevant location was cued on a trial by trial basis. We hypothesized that spatial attention would suppress low-frequency activity in contralateral sensorimotor and occipital cortex, when either modality was relevant (Macaluso and Driver, 2005). We focused exclusively on oscillatory activity in the cue-target interval, as any effects in this period reflects pure top-down influences of anticipatory attention, since they arise prior to any imperative target stimulus (and the central cue was not lateralized). We predicted that attention to modality (here vision or touch) would operate by modulating low-frequency activity in the sensory cortices associated with the task-relevant (versus irrelevant) modalities and hence via an analogous mechanism as for the spatial attention effects that we could study within the same experiment.

Methods

Participants

Thirteen right-handed healthy adult volunteers (aged 18 – 35, four female) were acquired through a local subject database. Approval for this study was given by UCL’s local research ethics committee and all participants gave informed written consent.

Task

Participants performed a visual or tactile task, where they reported only rare deviant stimuli (see below) in the currently task-relevant modality if appearing at the cued location for that trial (either left or right at 25 degrees eccentricity); see Eimer and colleagues (Eimer, 2001; Kennett et al., 2001; Eimer et al., 2002) for similar tasks and stimuli but focussing on evoked potentials in EEG. The standard stimuli consisted of single pulse LED-flashes in vision
(duration 200 ms), or electrical (index) finger stimulation in touch for 0.5 ms; while deviants were double pulse versions of the same stimuli. On different blocks of 88 trials either the visual or the tactile modality was task relevant and subjects were verbally instructed which modality was relevant prior to the beginning of each block. Each trial started with a centrally presented arrow cue stimulus (100 ms) that instructed the participant to attend either the left or right stimulus location for that trial (see Figure 1 for an illustration of experimental setup and task). The cue stimulus would be drawn pseudorandomly from one out of four different options (see below) and, importantly, was always presented bilaterally, with cue-color being the relevant feature instructing participants which side to attend to. Regardless of this spatial cue, and independent of which modality was task-relevant, on each trial just one peripheral stimulus was presented, either to the left or to the right equiprobably, and this could either be a visual or a tactile stimulus equiprobably. The task was to make a vocal response (saying ‘gap’) only if a deviant double-pulse stimulus was detected in the relevant modality at the cued location. Any deviant in the currently irrelevant modality required no response, and likewise for any deviant in the relevant modality but on the uncued side.

The experiment comprised 10 experimental blocks for most participants (only 8 for 2 participants due to practical constraints). Attended modality followed an ABBA or BAAB pattern across blocks. Starting modality was counterbalanced across participants. For each block of 88 trials, on 64 trials a standard stimulus was presented (either left or right, visual or somatosensory, with equal likelihood). Deviant (gap) stimuli were presented in the remaining, randomly intermingled 24 trials. Of these, 12 were on the cued side and in the attended modality (6 on the left, 6 on the right), 4 on the cued side but in the unattended modality (2 left, 2 right), the remaining 8 were uncued and either visual or somatosensory on the left or right.
Two or more training blocks were performed prior to the experiment, until performance was at or near ceiling. Practice blocks contained 32 trials: 16 standard stimuli (4 each side for each modality), 4 attended modality cued-side deviant stimuli, 4 ignored modality cued-side deviant stimuli and 8 stimuli uncued-side deviant stimuli (4 visual, 4 somatosensory).

**Stimulus details:**

Participants arms were placed palm-down on a board so that their index fingers were 600 mm from the participant’s eyes, 25° to left or right of straight ahead. A screen, 550 mm in front, received an image projected from outside (PRO xtraX LCD projector, Sanyo, Osaka, Japan) via a waveguide-porthole and two mirrors. A central grey fixation cross (0.9°) was continuously present on the screen during the experiment, 200 mm below horizontal straight-ahead. The cue stimulus comprised two triangles, one red, one blue, pointing in opposite directions either side of the fixation cross (i.e., ►+◄ or ◄+►; Fig. 1 top). Equiprobably, either arrowhead could be red, with the other blue. Thus there were four equiprobable cue-stimuli, all subtending 4.0° x 1.6° and participants were verbally instructed (and reminded prior to each block) which color indicated the imperative cue for them. Eight analysed participants were cued by the blue arrowhead and the remainder by red.

A peripheral stimulus, either visual or tactile (electrical) was presented unilaterally, after the cue-target interval (800 ms onset to onset). Visual stimuli were circles subtending 2.3°, 550 mm from the eyes, 25° to left or right of straight ahead (i.e., same as index fingers) and 10° below the level of the fixation cross. These visual stimuli were produced by external LEDs, with their light being conveyed via fibre optic cables to produce the circle when lit. Standard (“non-target”) visual stimuli comprised illumination of one circle for 200 ms. Rare “deviant” visual events, to be reported only for the cued side and only when vision was the attended modality, comprised one circle being flashed on-off-on for 85-30-85 ms (duration: 200 ms).
Tactile (electrical) stimuli were presented to either hand using two Digitimer DS7A constant current stimulators (Welwyn Garden City, U.K.); one connected to each index finger via a pair of gel Ag/AgCl electrodes (20 mm × 25 mm). Positive and negative electrodes were placed on the medial surface of the distal and proximal phalanx respectively. Stimulators were set to deliver 0.5 ms square-wave pulses. Detection threshold of each participant’s right index finger was determined using an informal staircase procedure. Experimental stimulus intensity was then 150% of this threshold (mean intensity = 4.2 mA). Standard (“non-target”) electrical stimuli comprised a single pulse, to one index finger, lasting 0.5 ms. Rare “deviant” electrical events, reported only when on the cued side and only when touch was attended, were two 0.5 ms pulses separated by a 70 ms gap presented to a single index finger.

Procedure

Participants sat comfortably in the magnetically shielded room and were familiarised with the stimulus equipment. Three head localisation coils were attached to anatomical landmarks (left and right pre-auricular points and nasion) to measure head position before and after each block. MEG data were subsequently recorded while subjects performed the task using 275 axial gradiometers (whole-head Omega 275 CTF MEG system; VSMmedTech, Vancouver, BC, Canada) with a sampling rate of 240 Hz given our focus on low frequency oscillations here (see Introduction).

Data processing

Data were analyzed using the Fieldtrip software package (http://www.ru.nl/fcdonders/fieldtrip/, see Oostenveld et al., 2011), a MATLAB-based toolbox for analysis of electrophysiological data. A semiautomatic artefact-rejection toolbox was run over the data to search for eyeblinks, muscle artefacts as well as any sudden jumps in
the signal caused by the electronic circuit controlling the SQUIDS (standard options in
Fieldtrip). The data were then screened visually to exclude trials or channels with excessive
power, using “rejectvisual”. Line noise was removed from 10s periods around each trial of
interest using a narrow-band notch filter. To correct for the interindividually varying head-
positions in the MEG sensor array (as traditionally the case with MEG recordings) the
artifact- and response-free data were interpolated to a common sensor array template using a
minimum-norm projection method (Knösche, 2002) as implemented in Fieldtrip (Oostenveld
et al., 2011) and used with default parameters. This procedure projects the sensor data onto
the individual participants head surface and reprojects it to a sensor array that has positions
(in this individual subjects based coordinate system) corresponding to the sample-averaged
head position in the MEG scanner. The minimum norm projection is not used here to make
inferences about the source-distributions, but solely serves as a way to represent an optimal
fit of the measured scalp topography in a head-centered coordinate system; the obtained
distribution on the head surface has little impact for the projection to the average sensor array
(for further details see Knösche, 2002 and Oostenveld et al., 2011 for the FieldtripToolbox).
Subsequently, planar gradients of the MEG field distribution were calculated using a nearest
neighbor method comparable to the method described elsewhere (Bastiaansen and Knösche,
2000). This metric effectively calculates a first order spatial derivative (in two planar
dimensions later aggregated by the vector norm, see below). Since MEG is maximally
sensitive to superficial tangential dipoles, and insensitive to deeper or radially oriented
sources (Hamalainen et al., 1993), the measured peak of activity can be expected to be in
fairly close spatial proximity to its cortical generator. Thus, while planar gradients will
attenuate signals originating from deeper sources (using the spatial derivative as here will
emphasize superficial sources even more) they are considered to allow an approximate
localization of the generators of the measured signals from topographies (see Bastiaansen and Knösche, 2000; Knösche, 2002).

Spectral analysis

In this study we were interested \textit{a priori} in low frequency oscillations in the anticipatory cue-target interval (see Introduction) and spectral analysis was therefore conducted between 2.5 and 50 Hz. To this end we used a Hanning taper of 400 ms window length which was Fourier-transformed and multiplied with the Fourier-transformed data-segments in the interval between -400 ms and 1200 ms around cue onset (multiplication in the frequency domain). This procedure is equivalent to a wavelet analysis except that the window length was kept constant across frequencies and a Hanning window was used instead of a Gaussian for more effective tapering of the data at the edges. The resulting time-frequency data were then sampled at steps of 50 ms and finally collapsed across vertical and horizontal planar gradients by taking the resultant vector length (see Bauer et al. 2006). For statistics concerning the attentional effects we used non-baseline corrected estimates of log power (from the vector length of planar gradients). For the display of the stimulus induced effects presented in Figure 1C (to show the mapping of planar gradients to occipital and sensorimotor regions), the pre-target baseline (in windows centered at -300 to -200ms before target onset) was estimated and a t-test was calculated within subjects (with individual trials as repetitions) as a comparison of poststimulus power vs baseline power, separately for each frequency bin and planar gradient sensor. The resultant t-statistics were then simply averaged across subjects (compare to Bauer et al. 2006 for a similar approach).

Results

Behaviour
Participants were able to perform the task quickly and accurately; 93.5 % of visual targets and 90.6 % of tactile targets were correctly detected at mean reaction times of 545 ms and 524 ms respectively. Only 1.4 % of non-targets in vision primary blocks and 1.3 % in touch primary blocks were erroneously responded to. No performance differences between vision primary and touch primary blocks approached significance by paired t-test (all t < 1.4, all p > 0.2).

**MEG**

Here we focused on attention related changes in low-frequency oscillatory activity in the cue-target interval. Such top-down changes in low-frequency-activity are known to arise primarily prior to and approaching stimulus onset, as shown in several previous studies assessing spatial attention effects in one modality only (Worden et al., 2000; Haegens et al., 2011). Accordingly, for the attentional contrasts, which were the main focus of this study, we focused on anticipatory changes within the cue-target interval and prior to stimulus onset. This allowed us to conduct analyses independent of the target-stimulus that was subsequently presented (tactile or a visual stimulus on the left or right). As one exception to this we present in Figure 1C the topographies of the visual and tactile stimulation effects (on beta-band suppression, from 15-30 Hz during the post-target-interval) – to familiarize the reader with the mapping of occipital and sensorimotor cortex that will become relevant in the subsequently presented figures on attentional modulation. Note that the planar gradient technique, a metric that represents local cortical activity underneath the sensors considered (Bastiaansen and Knösche, 2000), nicely separates activity induced by visual stimuli (bottom row in Fig 1C) and tactile stimuli (top row in Fig. 1C). The sensors marked in these topographies are chosen based on the MEG-manufacturers labelling (and correspond well with the shown lateralized stimulus induced effects) and are used to delineate left and right sensorimotor and occipital cortex in the subsequent figures 2-4. In all subsequently presented
analyses, however, we restricted the analysis to the pre-target stimulus period and could
therefore isolate pure top-down attentional effects on low-frequency oscillations, due solely
to which modality was task-relevant (blocked) and which location was currently task-relevant
(as cued at the start of each trial, see schematic timeline in Figure 1B and methods for details
on the cue stimulus). Figure 1A shows the experimental setup with electrical finger
stimulators located proximally to LEDs, on the left or right index finger. These visual or
tactile target stimuli were presented 800 ms after cue-onset. Cue-onset is denoted at 0 ms in
all subsequently presented figures and results.

Attention to Space

To investigate the effects of attention to a spatial location (left or right hemifield or finger),
we first calculated the main effect of log-transformed non-baseline-corrected power (on
synthetic planar MEG gradients) between the relevant conditions. Thus for the effect of
attention to space, we first calculated the comparison “Attend Left” minus “Attend Right”
pooled across the two attended modality (“Vision” or “Touch”) conditions. Figure 2 shows
time-frequency windows (Fig 2 A,B) and topographies (Fig 2 C,D) of this effect at sensors
overlying sensorimotor and occipital cortex as indicated. We also calculated the double
subtraction (AttLeft-AttRight)_{left sensors} minus (AttLeft-AttRight)_{right sensors} to combine the
results of both hemispheres into one value, as justified by the observed symmetry of the
contralateral spatial attention results (but for separate analysis of the hemispheres, see later
below).

Two related time-frequency patterns are clearly observable (see Fig 2, which plots t-values)
for the impact of spatial attention in the cue-target interval. A relative suppression of
broadband alpha- (7.5–15Hz) and beta-power (15-30Hz) arises between 400 and up to ~1000
ms (we restricted our analysis to 800ms to avoid containment of target-stimulus induced responses) following cue onset over sensorimotor cortex, contralateral to the attended side (relative suppression over right sensorimotor cortex and relative enhancement over left sensorimotor cortex, in the comparison of Attend Left minus Attend Right, see Fig 2 A and C); plus a relative suppression of primarily alpha- (7.5-15 Hz) and to some extent beta-power (~15-30 Hz) over occipital cortex contralateral to the attended hemifield (relative suppression over right occipital cortex, relative enhancement over left occipital cortex, see Fig 2 B and D).

While both sensorimotor and occipital cortex show evidence of lateralized relative suppression in both alpha- and beta-bands, topographies of the beta-band effect (Fig 2A) and time-frequency-profile (compare Fig 2 A and B) indicate a predominance over sensorimotor cortex for the higher beta-band and relative predominance over occipital cortex for the alpha-band. For the time-frequency windows highlighted in Fig 2 (which correspond to the windows for the topographies shown), the mean t-values for the spatial attention effect at sensorimotor sensors were $t=-3.6$ (p<0.005) for the beta-band and $t=-5.6$ (p<0.001) for the alpha-band. In sensors overlying occipital cortex the spatial attention effect was nearly significant for the beta-band ($t=-1.78$, p=0.0503) and highly significant for the alpha-band ($t=-5.6$, p<0.001). Thus, attention to a location in space suppresses the amplitudes of alpha-oscillations over occipital and sensorimotor cortex contralateral to the attended hemifield, extending prior work in unisensory studies (e.g., Worden et al., 2000; Bauer et al. 2006, Siegel et al. 2008, Jones et al., 2010; Haegens et al., 2011; van Ede et al., 2011) and clearly also modulates beta-oscillations overlying sensorimotor regions (Jones et al. 2010) and with a strong trend for occipital cortex (Siegel et al. 2008).

In the next step we investigated the effect of attention to space separately when either “Vision” was relevant (Figure 3 A-D), or when “Touch” was relevant (Figure 3 E-H).
Importantly, the result of this spatial-attention comparison is highly similar, regardless of which modality was relevant. When vision was relevant, the contralateral suppression of low-frequency oscillations did not only affect alpha-band activity over occipital cortex (Fig 3 B, D, t=-3.8 p<.0.01 for alpha, and t=-0.74, p>0.1 for beta), but also alpha- and beta-band activity over sensorimotor cortex (Fig 3 A,C, t=-3.1, p=0.005 for beta, and t=-4.7, p<0.001 for alpha). Conversely, when touch was relevant the contralateral suppression also involved not only sensorimotor (Fig. 3 E,G, t=-3.9, p<0.005 for beta and t=-5.4, p<0.001 for alpha) but also occipital sensors (Fig. 3 FH, t=-2.86, p<0.01 for beta, and t=-7.1, p<0.001 for alpha). Hence, alpha-band-activity was consistently modulated in sensorimotor and occipital regions as a consequence of spatial attention, whereas beta-band activity was modulated by spatial attention consistently in sensorimotor cortex, but not significantly in occipital cortex when vision was relevant. These results provide an oscillatory analogue of previous (non-oscillatory) reports that spatial attention in vision can affect sensorimotor cortex spatially, and vice-versa (Macaluso and Driver, 2005), thereby providing a new form of evidence that spatial attention can act in a multimodal fashion, with spatial attention for a task in one modality affecting low-frequency oscillations over sensory cortex ordinarily associated with the other modality.

Attention to Modality

Next we tested the main effect of attention to modality by the contrast “Attend Touch” minus “Attend Vision”. The statistical results of this comparison are shown in Figure 4. Analogously to the effect of spatial attention (but showing a distinct though partially overlapping topography), attention to modality leads to relative suppression of alpha-beta-band power over the sensory cortex corresponding to the task-relevant modality, compared to when that modality is task-irrelevant. In sensors overlying sensorimotor cortex (Fig. 4 A,C),
when touch was attended, alpha- and beta-band power was suppressed in a time-frequency-window from about 10 Hz to 30 Hz and from around 400 to 800 ms following cue onset (t=-2.22, p<0.05 for the beta-band and t=-2.15, p<0.05 for the alpha-band as in the highlighted windows and wide sensor selection as indicated in Figure 4). The frequency-distribution of this modality-selection effect is highly similar to that found for the spatial attention effect in sensorimotor cortex (see above). Over occipital cortex (Fig. 4 B,D), when touch was attended this resulted analogously in increased alpha-(t=2.20, p<0.01) but not increased beta-power (t=0.37, n.s.). This relative enhancement of occipital alpha-power in a condition when vision was irrelevant compared to when it was relevant mirrors the ipsilateral relative enhancement / contralateral relative suppression of alpha/beta-power for the case of spatial attention. Note that the reverse contrast “Vision – Touch” would lead to results with (numerically exact) inverted sign. That is, attention to vision would lead to a relative reduction for occipital alpha and a relative increase for sensorimotor alpha- and beta-oscillations.

Spatial attention effects for sensors showing modality-selectivity

To rule out potential concerns that due to the relatively wide sensor selection spatial attention effects would only appear to be prominent in modality selective regions, our final step was to select those sensors that each show highly significant (at p<0.01) effects of attention to modality and then to investigate if these same modality-selective sensors would also show clear effects of spatial attention with either modality relevant, as we anticipated. Please note that these sensors were thus selected by a criterion (modality selectivity) that was independent of subsequent tests for spatial attention effects and that by definition they show a modality selectivity (i.e. a significant preference for either touch or vision being the relevant modality). As expected, the modality-selection criterion highlighted sensors over parieto-
occipital or sensorimotor cortex, respectively, for attending vision or touch (see highlighted
sensors in Figure 5E for the alpha band). The key outcome is that despite this modality-
selectivity, the highlighted visual-preferring parieto-occipital sensors showed significant
effects of spatial attention (Fig 5C-D) when *either* modality was task-relevant, for the visual
*or tactile* task; and analogously for the touch-preferring sensorimotor sensors, which showed
spatial attention effects for the tactile *or visual* task (see Fig 5A-B). Thus, in terms of pure
top-down attentional effects in the cue-target interval, sensorimotor sensors showed relative
low-frequency suppression when attending to touch *and* when attending contralaterally *for
either modality*; while parieto-occipital sensors analogously showed low-frequency
suppression when attending to vision *and* when attending contralaterally *for either modality.*

These results in the alpha-band were confirmed statistically by an ANOVA on the group data
for which means are plotted in Figure 5. An initial 2 x 2 x 2 ANOVA (Hemisphere: left/right,
Spatial attention: contralateral/ipsilateral, Attention to Modality: Touch/Vision) found no
interactions with factor ‘Hemisphere’ when re-coding attended side in terms of contralateral
or ipsilateral, rather than left or right hemifield/finger (all p>0.16). Accordingly we next
pooled the data across hemispheres, again with attended side coded as contralateral or
ipsilateral, in a 2x2 ANOVA with factors of ‘Spatial attention’ and ‘Relevant Modality’. For
alpha at sensorimotor sensors, this revealed main effects of spatial attention (lower alpha for
contralateral attention, $F_{(1,12)}=36.31, p<0.001$) and of attended modality (lower alpha when
touch was task-relevant, $F_{(1,12)}=11.84, p<0.01$), plus an interaction ($F_{(1,12)}=6.39, p<0.05$) due
to a somewhat stronger spatial attention effect with touch relevant (although note that the
spatial attention effect remained significant here with vision task-relevant also, at $p<0.01$, see
also Figure 5A,B).

Analogously, for alpha at occipital sensors, there were main effects of spatial attention (lower
alpha for contralateral attention, $F_{(1,12)}=22.50, p<0.01$) and of attended modality (lower alpha
now when *vision* was task-relevant, $F_{(1,12)}=15.60$, $p<0.01$, and a trend for an interaction

$(F_{(1,12)}=4.28$, $p=0.06$) that was not quite significant.

The beta band (Fig 5F-J) showed a similar but statistically less robust pattern than the alpha-band shown in Fig 5, in line with beta-frequencies being more prominent at sensorimotor than occipital sensors, whereas the alpha band was implicated for both sites. The ANOVA results for the beta-band (with the sensor selection as above – chosen by modality effects in the alpha-band as there were no modality selective sensors e.g. in left parieto-occipital cortex in the beta-band, yet the difference had a similar topology) where the following: In sensorimotor regions (as depicted in figure 5, collapsed over the hemispheres) both Attention to Location and Modality effects were significant ($F=14.4$, $p<0.01$ and $F=8.9$, $p<0.05$, respectively), as was the interaction of both ($F=7.1$, $p<0.05$). In occipital sensors the effect of Attention to Location was significant ($F=8.15$, $p<0.05$) and while the effect of Attention to Modality was not ($F=0.69$, $p>0.1$), the interaction was also significant here ($F=6.37$, $p<0.05$).
Discussion

Our study adds to a growing literature that increasingly emphasizes the role of low-frequency oscillations (particularly alpha-band) for attentional modulations arising in an anticipatory interval prior to onset of a target stimulus (e.g., Foxe et al., 1998; Worden et al., 2000; Fu et al., 2001; Thut et al., 2006; Trenner et al., 2008; Lakatos et al. 2008; Haegens et al., 2011; van Ede et al., 2011). Such oscillations have been implicated in spatial attention, with most studies (though not all: Jones et al., 2010; Haegens et al., 2011; van Ede et al., 2011) focusing on alpha-band modulations for parietal-occipital cortex related to visual processing. Alpha-oscillations have also been implicated in modality selection (Foxe et al., 1998), for audio-visual cases, with a focus on parietal-occipital oscillations related to visual processing. In the present study we jointly investigated spatial and modality selection effects simultaneously in the visual and tactile modality, and report attention related modulations in alpha- and beta-bands over sensorimotor and occipital cortex as measured with planar gradient MEG sensors.

We found not only that attention towards or away from vision as a relevant modality modulates parieto-occipital low-frequency oscillations, as previous studies had shown; but also that attending towards or away from touch as a relevant modality analogously modulates sensorimotor alpha- and beta-oscillations (Figure 4). In this sense, modality-selection behaved ‘symmetrically’, i.e. both occipital and sensorimotor regions were modulated, in a converse see-saw manner, suggesting that alpha-modulation related to modality selection is a more general phenomenon that does not only apply to parieto-occipital cortex.

We also found that spatial attention to one or other side led to contralateral/ipsilateral relative increases/decreases in low-frequency power, as expected. Importantly we were able to show further that these preparatory spatial attention effects were found in the present visual-tactile...
paradigm over both occipital and sensorimotor cortex, when *either* modality was attended (Figures 2 and 3). Finally, even when selecting planar gradient sensors that showed a significant preference for one or other modality being task-relevant (Fig 5), and that had the expected corresponding localisation over parieto-occipital (for vision relevant) or sensorimotor (for touch relevant) regions, we still found that spatial attention effects arose for these sensors with either modality being attended. Thus attention to space is not constrained to the currently selected modality, but operates also on the task-irrelevant modality and therefore attention to space and modality can operate in parallel.

This had been previously shown for (target-) stimulus related responses using behavioural, ERP, and fMRI measures (Spence and Driver, 1998; Eimer and Driver, 2001; Kennett et al., 2001; Eimer et al., 2002; Talsma et al., 2010), but here we show it also for the pure top-down effect manifested in low-frequency oscillations measured with MEG.

Sensorimotor and parieto-occipital regions thus seem to act analogously, with respect to low-frequency modulation of activity due to spatial attention and due to modality selection. Nonetheless there were two notable differences. First, while spatial attention effects were pronounced in the alpha-band (7.5-15 Hz) for both sensorimotor and (parieto-) occipital sensors, effects in the former clearly extended further into the beta-band (see Fig 2). For modality selection (see Fig 4), it was also the case that effects over sensorimotor cortex were more dominant in the beta-band than in alpha, though present for both. In occipital cortex, the results in the beta-band were somewhat less consistent. While in parieto-occipital regions (as selected post-hoc by modality-selective effects) spatial attention yielded a significant modulatory effect and in more posterior sensors (selected a priori) there was a strong trend
effects on modality selection were almost absent. These tentative differences for
the spectral consequences of attentional modulation in occipital versus sensorimotor cortex
may relate to previous discussions about resonance frequencies in these different regions
(Hari and Salmelin, 1997; Gaetz and Cheyne, 2006; Rosanova et al., 2009).

Recent studies (Buffalo et al., 2010; Maier et al., 2010) indicate that low-frequency activity
(predominantly alpha--band) in visual cortex may predominantly originate from the deep
(infragranular) layers innervated by feedback projections from higher areas (Felleman and
Van Essen, 1991). Such top-down influences would accord with alpha-modulations being
prominent in the anticipatory period prior to target onset (Worden et al., 2000; Haegens et al.,
2011), as found here. Jensen and Mazaheri (Jensen and Mazaheri, 2010) propose that such
modulations of low-frequency activity in sensory cortex are predominantly caused by
inhibitory mechanisms, such that during the troughs of strong alpha -oscillations (when the
membrane is hyperpolarized) an increase of alpha- oscillations leads to reduced excitability
of the neuronal population with respect to incoming afferent information.

While often alpha- and beta-oscillations seem to behave in a correlated fashion with respect
to bottom-up and top-down inputs (e.g. Hoogenboom et al. 2006; Siegel et al. 2008; Jones et
al. 2010), there are also notable differences: Despite the fact that beta-oscillations are often
suppressed following stimulus processing (Hoogenboom et al. 2006; Bauer et al. 2006),
enhanced levels of beta-activity in widespread networks are often correlated with enhanced
task performance related to sensorimotor integration and decision making (Gross et al. 2004;
Donner et al. 2007). Furthermore, on the neurophysiological level, Jensen et al. (2005)
provided evidence for a dissociation between alpha-and beta-rhythms in response to
GABAergic pharmacological manipulation in sensorimotor cortex. Ziegler et al. (2010)
argued that the sensorimotor beta-rhythm may reflect a superposition of two different alpha-
rhythms in sensorimotor cortex. Clearly, more research is needed to fully understand the
differential nature of the neurogenesis as well as the more functional aspects of alpha- and
beta-oscillations in sensorimotor and occipital cortex.

While there were strong communalities for the effects of spatial attention (Fig 2) and
modality selection (Fig 4) in terms of their spectral signature (especially in sensorimotor
cortex) and the topographies, these effects were not necessarily identical. In particular, in
occipital and parieto-occipital regions, attention to modality effects did not modulate beta-
power but a mild effect of spatial attention on parieto-occipital beta-oscillations was
observed. However, since relevant modality was assigned on a block-by-block basis here,
whereas attended side was cued on a trial-by-trial basis, future extensions of the current
paradigm could investigate the possible basis of the potential topographical and spectral
differences, for instance by reversing which factor is cued and which blocked.

Furthermore, the interaction effect of spatial attention and attention to modality, that showed
a general tendency for stronger spatial attention effects when touch was the relevant
modality, compared to when vision was the relevant modality (in both sensorimotor and
occipital cortex) may be attributable to slight differences in task difficulty or attentional load
for the tactile versus visual task. While the behavioral results are not significantly different
between these task, subjects tentatively responded slower and committed more errors in the
tactile compared to the visual task (nonsignificant).

To conclude, this MEG study shows that spatial attention affects not only occipital but also
sensorimotor regions, via top-down-modulation of low-frequency alpha- and beta-
oscillations, when either modality is task relevant in a visuo-tactile situation. At the same
time, modality selection can likewise affect not only parieto-occipital alpha oscillations
related to vision, but also sensorimotor alpha- and beta oscillations. The results show further
that the spectral concentration of these effects may reflect resonance properties in the affected
sensory areas - predominantly alpha for occipital cortex, but alpha- and beta- for
sensorimotor areas, (Rosanova et al., 2009). This spectral nature was similarly distinctive
here for either site in the case of both spatial attention and modality selection influences.
Thus, for vision and touch alike, spatial attention and modality selection both involve top-
down modulation of low-frequency oscillations, though the exact spectral patterns differ
regionally.

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Figure Legends

Figure 1: Task schematics

(A): Experimental task setup. Participants fixate centrally, peripheral stimuli are presented to left or right, with tactile and visual stimuli in close spatial proximity.

(B): Timeline: Each trial starts with the presentation of a central cue for 100ms, followed by a 700ms empty interval, then presentation of either a tactile stimulus (0.5ms electrical shock) or visual stimulus (LED 200ms). Note that our MEG analyses focus on the cue-target interval, prior to target stimulus, in order to highlight pure top-down effects of preparatory attention (in absence of peripheral target stimulus related effects).

(C): Mapping of the visual or tactile (target) stimulus induced responses (beta-band suppression, 15-30 Hz) on the planar gradients. Left tactile stimuli suppress beta-activity in predominantly right sensorimotor channels, right tactile stimuli in left sensorimotor channels. Visual stimuli suppress beta-activity in bilateral occipital channels. Note the spatial specificity of these response patterns. These sensors are used and labelled as ‘sensorimotor’ and ‘occipital’ channels throughout figures 2-4.

Figure 2: Attention to Spatial Location (Main Effect)

Topographies and time-frequency-representations of the spatial attention effect (regardless of modality judged). (A, B): Time-frequency plot of contralateral attention effects: (AttLeft-AttRight)_{left sensors} minus (AttLeft-AttRight)_{right sensors}. (A) plots these for the sensors over somatosensory cortex highlighted in (C), while (B) shows this for the sensors over occipital cortex highlighted in (D). (C): Topography of t-values for attending left minus right in the beta-band of 15-30Hz (A), and (D) the alpha-band of 7.5-15 Hz (B), over the time-frequency
windows marked in A and B above, respectively. Topographies are averaged over the time-frequency windows as marked in (A for C, B for D). Sensor selection marked in C and D for time-frequency plots in A and B, respectively. All plots show t-values.

**Figure 3: Attention to Spatial Location under Vision and Touch**

Topographies and time-frequency-representations of spatial attention effects shown analogously to Figure 2, but now separately for vision or touch being task-relevant.

**(A-D):** Spatial attention effect when Vision relevant;

**(A, B):** Time-frequency plot of contralateral attention effects: \((\text{AttLeft-AttRight})_{\text{left sensors}}\) minus \((\text{AttLeft-AttRight})_{\text{right sensors}}\) for sensorimotor (A) and occipital sensors (B), marked in C and D, respectively. **(C, D):** Topography of t-values attending left minus right for beta (C) and alpha (D) activity, averaged over time-frequency windows marked in A and B, respectively.

**(E-H):** Attention to Space when Touch relevant.

**(E, F):** Time-frequency plot of contralateral attention effects: \((\text{AttLeft-AttRight})_{\text{left sensors}}\) minus \((\text{AttLeft-AttRight})_{\text{right sensors}}\) for sensorimotor (E) and occipital sensors (F), marked in G and H, respectively. **(G, H):** Topography of t-values attending left minus right for beta (G) and alpha (H) activity, averaged over time-frequency windows marked in E and F, respectively. All plots show t-values.

**Figure 4: Attention to Modality**

Topographies and time-frequency-representations of modality-relevance effect (regardless of attended side). **(A, B):** Time-frequency plot of alpha-and beta-suppression for somatosensory (A) and occipital sensors (B); sensor selection marked in C and D, respectively. All plots
show t-values. \textbf{(C, D):} Topography of attending touch minus vision for (C) beta and (D) alpha bands, averaged over time-frequency windows marked in A and B, respectively.

\textbf{Figure 5: Attention to Space and Modality at modality-selective sensors}

Activity profiles for \textbf{(A-D)} alpha-activity (7.5-15 Hz, for 0.4-0.8s into the cue-target interval) at sensors selected to show a preference (significance exceeding \( p<0.01 \)) either for touch being task-relevant, which arose at sensorimotor sensors \textbf{(A, B)}, or for vision being task-relevant, which arose at parieto-occipital sensors \textbf{(C, D)} as marked in \textbf{(E)} the middle headview (occipital red, sensorimotor blue) which also depicts the topography for the contrast ‘attend touch minus attend vision’ (in the alpha-band). The bar plots show the mean log-transformed alpha-power of magnetic induction in planar gradients (hence negative log values) for the four different attentional conditions (‘Touch Left’, ‘Touch Right’, ‘Vision Left’, ‘Vision Right’) in the preparatory cue-target interval. The conditions are plotted relative to the lateral sensor positions (‘Touch Right’ becomes ‘TouchContra’ for left sensors). Asterisks indicate significant (\( p<0.05 \)) attention to modality and location effects (by paired t-test, which are found for every case. In particular, note that spatial attention effects are significant even in sensors that show a clear preference for the other modality. \textbf{(H-J)}

Same as above \textbf{(A-E)} but now for the beta-band (15-30 Hz, for 0.4-0.8s into the cue-target interval). While all contrast in sensorimotor sensors are also significant for the beta-band, in parieto-occipital sensors they were not. Since effects of modality selection in the beta-band were not significant anywhere in sensors over parieto-occipital cortex, the sensor selection \textbf{(J)} here was therefore adopted from the contrast of attention to touch – vision in the alpha-band \textbf{(E)}.
Figure 1

A

B

Laterality cue  
Target stimulus  
Vis: 200 ms, Tac: 0.5 ms

Time (ms)

C

Target stimulus induced responses (15-30 Hz)

Left tactile stim  
Right tactile stim

Left visual stim  
Right visual stim

t-value
Main Effect of Attention to Location

Figure 2
Figure 3

Attention to Location under Vision

A. Attention Location Somatosens

B. Attention Location Occipital

C. Att Left minus Right BETA

D. Att Left minus Right ALPHA

Attention to Location under Touch

E. Attention Location Somatosens

F. Attention Location Occipital

G. Att Left minus Right BETA

H. Att Left minus Right ALPHA
Main Effect of Attention to Modality

Figure 4
Alpha-Band (7.5-15 Hz)

Figure 5