Occipital Alpha and Gamma Oscillations Support Complementary Mechanisms for Processing Stimulus Value Associations

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Abstract

■ Selective attention is reflected neurally in changes in the power of posterior neural oscillations in the alpha (8–12 Hz) and gamma (40–100 Hz) bands. Although a neural mechanism that allows relevant information to be selectively processed has its advantages, it may lead to lucrative or dangerous information going unnoticed. Neural systems are also in place for processing rewarding and punishing information. Here, we examine the interaction between selective attention (left vs. right) and stimulus's learned value associations (neutral, punished, or rewarded) and how they compete for control of posterior neural oscillations. We found that both attention and stimulus–value associations influenced neural oscillations. Whereas selective attention had comparable effects on alpha and gamma oscillations, value associations had dissociable effects on these

neural markers of attention. Salient targets (associated with positive and negative outcomes) hijacked changes in alpha power—increasing hemispheric alpha lateralization when salient targets were attended, decreasing it when they were being ignored. In contrast, hemispheric gamma-band lateralization was specifically abolished by negative distractors. Source analysis indicated occipital generators of both attentional and value effects. Thus, posterior cortical oscillations support both the ability to selectively attend while at the same time retaining the ability to remain sensitive to valuable features in the environment. Moreover, the versatility of our attentional system to respond separately to salient from merely positively valued stimuli appears to be carried out by separate neural processes reflected in different frequency bands. ■

INTRODUCTION

An organism operating in a complex environment with limited processing capacity must balance competing requirements. Processing of information associated with relevant stimuli must somehow be prioritized at the expense of processing of irrelevant information. However, stimuli with value associations must be able to capture resources to achieve an expedited processing state (Baluch & Itti, 2011). The brain thus needs to engage in enhanced processing both voluntarily and in a manner driven by learned value associations. In this study, we investigated how these two processes integrate.

The amplitude of alpha-band activity (8–12 Hz) changes with voluntary attention to selectively engage or suppress task-relevant or -irrelevant information, respectively (Jensen & Mazaheri, 2010; Snyder & Foxe, 2010). Anticipation of visual targets decreases alpha activity, whereas anticipation of visual distractors increases it (Gould, Rushworth, & Nobre, 2011; Handel, Haarmeier, & Jensen, 2011), and covert attention to one hemifield decreases

parieto-occipital alpha power contralateral to attention while increasing it ipsilaterally (Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Worden, Foxe, Wang, & Simpson, 2000). Alpha is under top–down control from high-order visual regions (Bastos et al., 2015), including the dorsal attention network (Corbetta & Shulman, 2002), which has been shown to play a role in voluntary attention (Nobre, Gitelman, Dias, & Mesulam, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999). Inhibition of dorsal network regions with TMS disrupts both voluntary attention and alpha modulation (Marshall, O'Shea, Jensen, & Bergmann, 2015).

In contrast, gamma-band (40–100 Hz) power increases as a result of voluntary attention (Koelewijn, Rich, Muthukumaraswamy, & Singh, 2013; Fries, Reynolds, Rorie, & Desimone, 2001) in a hemifield-specific manner (Siegel, Donner, Oostenveld, Fries, & Engel, 2008) that is behaviorally relevant (Hoogenboom, Schoffelen, Oostenveld, & Fries, 2010). Increased gamma-band synchronization likely emerges from a bottom–up drive to the visual system (Bastos et al., 2015; van Kerkoerle et al., 2014) and results in increased neuronal gain, supporting efficient transfer of information up through a cortical hierarchy (Tiesinga, Fellous, & Salinas, 2004; Salinas & Sejnowski, 2001). Thus, increases in gamma power likely

reflect expedited active processing of visual stimuli (Tallon-Baudry & Bertrand, 1999).

Attention can be biased by learned associations with stimuli (Theeuwes & Belopolsky, 2012); stimuli with positive associations become both easier to select and harder to ignore (Anderson, Laurent, & Yantis, 2011; Della Libera & Chelazzi, 2009), and presentation of rewarding information in a task-irrelevant context impedes task performance (Hickey, Kaiser, & Peelen, 2015; Krebs, Boehler, & Woldorff, 2010). Stimuli with negative associations also capture attention (Fox et al., 2000); pictures containing negative objects elicit longer fixation times and increased recall accuracy (Humphrey, Underwood, & Lambert, 2012), and negative faces impair performance on a facial feature counting task (Eastwood, Smilek, & Merikle, 2003). The attention and reward systems are likely to be tightly coupled (Baluch & Itti, 2011); value history and spatial attention induce highly similar biases in visual cortex in both monkey (Stănişor, van der Togt, Pennartz, & Roelfsema, 2013) and human (Serences, 2008). It may even be the case that rewards and punishments are a dominant factor in optimizing selective attention in order for an organism to optimize its interaction with the environment (Chelazzi, Perlato, Santandrea, & Della Libera, 2013; O'Brien & Raymond, 2012). Given this putative tight coupling of value and attention in brain and behavior, we hypothesize that the electrophysiological signatures of selective attention are influenced by value associations.

In this study, participants performed a visual cueing task where attention and value were orthogonally manipulated. Participants first performed a conditioning manipulation where they learned associations between stimuli—Chinese characters—and rewards or losses (Figure 1A). Stimuli acquired both a salience (some symbols acquired a value connotation, others served as controls) and a specific valence (reward or loss). Then participants performed a Posner-type attentional cueing task during MEG recordings where the conditioned stim-

uli served as targets and distractors. Participants were told that the learned value associations would apply during this test phase (i.e., every presentation of a value-salient stimulus resulted in a reward or loss for them, irrespective of task performance) to prevent extinction. However, the task was to detect a contrast change in the cued stimulus and thus required only voluntary attention. Thus, attention and value were orthogonally manipulated.

Stimulus–value associations may interact with attention to influence posterior neuronal oscillations in three distinct ways. First, because stimuli with learned connotations—both rewarding and punishing—need to be prioritized, it may be that stimuli influence alpha and gamma according to their salience. Second, because attentional effects have been shown for negative stimuli specifically (Eastwood et al., 2003; Fox et al., 2000), valence may play a role. Third, the current focus of selective attention, that is, the relevance of a stimulus at the current time, may exert an influence. This design enabled us to test these three factors in parallel; the first by comparing the oscillatory responses to positive and negative stimuli with neutral stimuli, the second by comparing positive and negative stimuli to each other, and the third by comparing targets with distractors.

METHODS

Participants

Twenty-eight participants (11 men), aged 23 ± 2.7 years (mean ± SD) participated in the experiment. Participants were right-handed, had no prior knowledge of any Chinese language, and had normal or corrected-to-normal vision. All experiments were carried out in accordance with the Declaration of Helsinki and following ethical approval by the local ethics board (CMO regio Arnhem-Nijmegen, CMO2001/095). A technical error resulted in experimental data not being available for one participant, and one participant was excluded because of excessive eye movements

Figure 1. Experimental paradigm. (A) Representative stimulus set. During the association phase, two Chinese characters were paired with a positive value, two with a negative value, and two with no value ("neutral" stimuli). This allows examination of the effects of stimulus salience (by comparing positive and negative stimuli with neutral) and of stimulus valence (by comparing positive with negative). (B) Example trial of the learning phase. Participants were repeatedly shown Chinese characters, which were consistently paired either with a positive value, a negative value, or no value via visual and auditory feedback. (C) Example trial of the testing phase. Participants were instructed to pay attention to the symbol on the cued side and report when that symbol changed contrast.
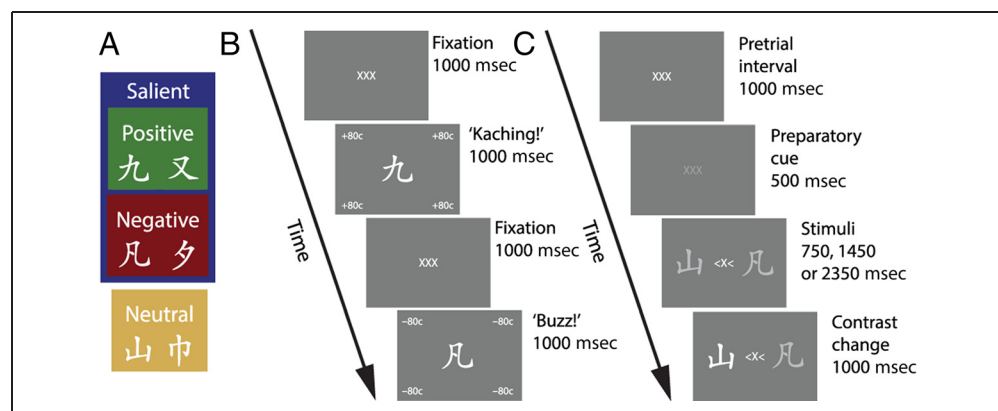
during the MEG recordings (>90% of all trials). All sensor-level and statistical analyses were therefore conducted on the remaining 26 participants. For one further participant, no structural MRI scan was acquired. All source analysis was therefore conducted on 25 participants.

Procedure

There were two phases to the experiment: a training phase and a test phase. During the initial training, participants learned associations between Chinese characters and positive, neutral, or negative outcomes. Then, immediately afterwards, they performed a cued spatial attention task using these symbols while MEG data were acquired.

The training phase was conducted in a dimly lit sound-attenuated room, without electrophysiological recordings. Stimulus–reward associations were randomized over participants. Figure 1A shows one possible set of stimulus–reward associations. As depicted in Figure 1B, the trial sequence consisted of white stimuli presented on a gray background. Each trial started with a fixation cross that was displayed for 1 sec. Then one of six different stimuli was presented, followed by both visual and auditory feedback. Two stimuli were associated with positive feedback (+80 cents, "kaching!" sound), two were associated with negative feedback (−80 cents, "buzz" sound), and two were associated with neutral feedback (0 cents, "beep" sound). In this way, stimuli could both become associated with a salient outcome, with a specific valence. Participants were instructed to memorize the stimuli and their associated values. Each stimulus was presented 12 times. At the end of the learning phase, participants were tested on the stimulus–value associations.

Participants performed the subsequent test phase while MEG was acquired. Figure 1C shows one representative trial. At the beginning of each trial, three white fixation crosses were presented for 1000 msec, before dimming for 500 msec to instruct the participant to fixate on the central cross, to refrain from blinking, and to signal the upcoming stimuli. Two stimuli were then presented 8° of visual angle to the left and right of the fixation cross, simultaneously with a spatial cue consisting of two arrows flanking the central fixation cross. After an interval of 1450 msec (47% of trials) or 2350 msec (40%), one stimulus changed contrast. On 13% of trials, the contrast change occurred after 750 msec; these "catch" trials were to ensure that participants would begin directing covert attention rapidly following the cue. Data from these short-interval trials were not analyzed. Contrasts could either increase or decrease with equal probability. On 95% of trials, the cued stimulus changed contrast, and on 5% of trials, the uncued stimulus changed contrast. Participants were instructed to indicate the direction of contrast change of the cued stimulus as quickly as possible with a button press using either the index or middle finger of the right hand (change direc-

tion/finger mapping was randomized across participants). Participants were instructed not to respond when the uncued stimulus changed contrast and data from these trials were also not analyzed. Participants completed eight blocks of 72 trials. Total task time was approximately 50 min.

Crucially, participants were informed before commencement of the test phase that the previously learned symbol–reward associations would apply during the test phase, that is, that each presentation of a given symbol—whether in the cued or uncued location—would result in financial reward, financial penalty, or neither (nominal extinction). This was done to directly test the effects of reward associations on the neural signals when reward and attention were orthogonalized (i.e., when task performance did not influence financial outcome).

MEG Data Acquisition

MEG data were recorded from participants in the seated position using a CTF 275-channel axial gradiometer MEG system (CTF MEG systems, VSM MedTech Ltd., Coquitlam, Canada). The MEG data were sampled at 1200 Hz after a 300-Hz low-pass filter was applied. During recordings, the positions of three fiducial markers (left and right ear canals and nasion) were continuously monitored in real time via an in-house head localization software (Stolk, Todorovic, Schoffelen, & Oostenveld, 2013). This tool was used to adjust the participants' head positions in the breaks between blocks to ensure minimal head movement over the course of the experiment. Electrocardiogram and horizontal and vertical EOG were recorded using bipolar electrode pairs.

MEG Data Analysis

All MEG analyses were performed using the MATLAB FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). Data were demeaned, a linear trend was fitted and removed, and line noise was removed using a discrete Fourier transform approach at the principal (50 Hz) and first and second harmonic (100 Hz, 150 Hz) frequencies. Data were preprocessed using automatic artifact detection methods to remove trials containing eye blinks and horizontal eye movements (assessed using the horizontal and vertical EOG channels, respectively) and SQUID jumps and muscle artifacts (assessed using the MEG channels).

Synthetic planar gradients were calculated to facilitate interpretation of MEG sensor topographies. Planar gradient maxima are known to be located above underlying neural sources (Bastiaansen & Knösche, 2000; Hari & Salmelin, 1997). First, the axial gradiometer data were converted to orthogonal synthetic planar gradiometer pairs, then time frequency representations of power were computed, and finally the powers of the pairs were combined for a given sensor pair location. Oscillatory power for low frequencies

was estimated for the 2–30 Hz frequency bands using a fast Fourier transform. A sliding time window approach was used to extract a 500-msec data segment every 50 msec; data segments were multiplied with a Hanning taper before computing the fast Fourier transform. Power for high frequencies was estimated from 30 to 140 Hz in steps of 5 Hz. Data segments of 200 msec were extracted every 50 msec and multiplied with a set of seven orthogonal Slepian tapers to produce a frequency smoothing of ±20 Hz.

For the alpha band analysis, we focused on the 8–12 Hz frequency range (Marshall et al., 2015; Okazaki et al., 2015; Bonnefond & Jensen, 2012; Sauseng, Klimesch, Gerloff, & Hummel, 2009; Sauseng et al., 2005). For gamma-band analysis, we chose a range of 45–65 Hz based on inspection of the grand-averaged data. We also preselected relevant time windows. For both frequency bands, a 750-msec window of interest was selected from 450–1200 msec following the onset of the visual stimuli. This time window was used to avoid contamination by cue-related and stimulus onset-related phase-locked activity (because we used a 500-msec sliding time window for the alpha data and the first change moment could occur at 1450 msec postcue). We used the same window for the gamma to compare the alpha and gamma data.

Statistics

The power of time–frequency windows of the MEG data was averaged across two predefined ROIs consisting of all parietal and occipital sensors in each hemisphere. Average oscillatory power values were calculated for these two ROIs for each of the nine conditions described below. We then combined these two ROI values into a single measure for each condition using the lateralization index, which effectively controls for individual differences in overall power by normalizing to the sum of the power values in the two ROIs (Haegens, Handel, & Jensen, 2011; Thut et al., 2006) according to the formula

$$
\begin{aligned}
\mathrm{ALI}_j = (\mathrm{Power}_{j,\,\text{ipsilateral hemisphere}} \\
- \mathrm{Power}_{j,\,\text{contralateral hemisphere}})/ \\
\mathrm{Power}_{j,\,\text{ipsilateral hemisphere}} \\
+ \mathrm{Power}_{j,\,\text{contralateral hemisphere}})
\end{aligned}
$$

Here, "contralateral" and "ipsilateral" refer to the direction of attention. The three possible target values (positive, negative, neutral) and three possible distractor values (positive, negative, neutral) created a total of nine possible experimental conditions. For both alpha and gamma bands, lateralization index values were calculated for each participant and each of the nine conditions and entered into a 3 × 3 repeated-measures ANOVA (rmANOVA). Greenhouse–Geisser correction was performed where necessary. Post hoc analysis was performed using paired-samples t tests. Statistical analyses were performed using SPSS and MATLAB.

Source Analysis

To explore the underlying sources generating the effects of value on alpha and gamma, we performed a source analysis using DICS beamforming (Gross et al., 2001). Using an MNI template brain, a three-dimensional grid with 8-mm spacing was constructed, mirror symmetric about the sagittal midline. The template brain was then warped to the individual participant's anatomical MRIs, and the inverse warp was applied to the grids. This produces subject-specific grids aligned in a common (MNI) space.

Source analyses were conducted separately for each frequency band of interest. For the alpha band, a 1000-msec window was used from the cue target interval, 300–1300 msec after the onset of the stimuli. From all artifact-free trials, the cross-spectral density was computed using a Slepian taper set consisting of three orthogonal tapers, with a 10-Hz center frequency and 2-Hz spectral smoothing. Note that the use of a 1000-msec window for the alpha-band source analysis contrasts the sensor-level data where a 750-msec window was used. The longer window ensures that frequency smoothing can be controlled to precisely an 8–12 Hz band for comparability with the sensor-level analysis. For the gamma band, a 750-msec window was used from 450 to 1200 msec after stimulus onset, with a 55-Hz center frequency and 10-Hz smoothing, that is, at 45–65 Hz band for comparability with the sensor-level analysis.

The common spatial filter was then used to estimate average power for each experimental condition: attention (left, right), target value (positive, negative, neutral), and distractor value (positive, negative, neutral). From these data, we then computed attentional lateralization index (ALI) for each pair of symmetric grid points in the left and right hemispheres, according to the formula

$$
\begin{aligned}
\mathrm{ALI}_j = (\mathrm{Power}_{j,\,\text{ipsilateral hemisphere}} \\
- \mathrm{Power}_{j,\,\text{contralateral hemisphere}})/ \\
\mathrm{Power}_{j,\,\text{ipsilateral hemisphere}} \\
+ \mathrm{Power}_{j,\,\text{contralateral hemisphere}})
\end{aligned}
$$

We then computed the grand average for each reward condition and extracted the "peak" grid point displaying maximum lateralization in each value condition. We then interpolated these lateralization maps to a high-resolution anatomical template for visualization. Finally, we looked up the peak locations in the AAL atlas (Tzourio-Mazoyer et al., 2002) to determine the anatomical region in which lateralization was strongest for each frequency band an value condition.

RESULTS
Salient Value-associated Targets Increased Alpha Lateralization

The spatial attention and reward paradigm is shown in Figure 1. The MEG data were acquired during the testing phase where we presented the target and distractor

Figure 2. Alpha lateralization demonstrates sensitivity to stimulus salience, but not to stimulus valence. (A) Hemispheric alpha lateralization index, averaged across all conditions. Clear, band-limited attentional lateralization is visible in the alpha band, persisting until the contrast change. (B) Topographies of attentional lateralization in the 8–12 Hz band for each value of target and distractor. (C, D) Both positive and negative targets (i.e., salient targets) produced increased alpha lateralization compared with neutral targets. (E, F) Both positive and negative distractors (i.e., salient distractors) reduced alpha lateralization compared with neutral distractors. Error bars indicate standard errors of the mean. Asterisks denote statistical significance; $*p < .05$, $**p < .01$, $***p < .001$, $****p < .0001$.
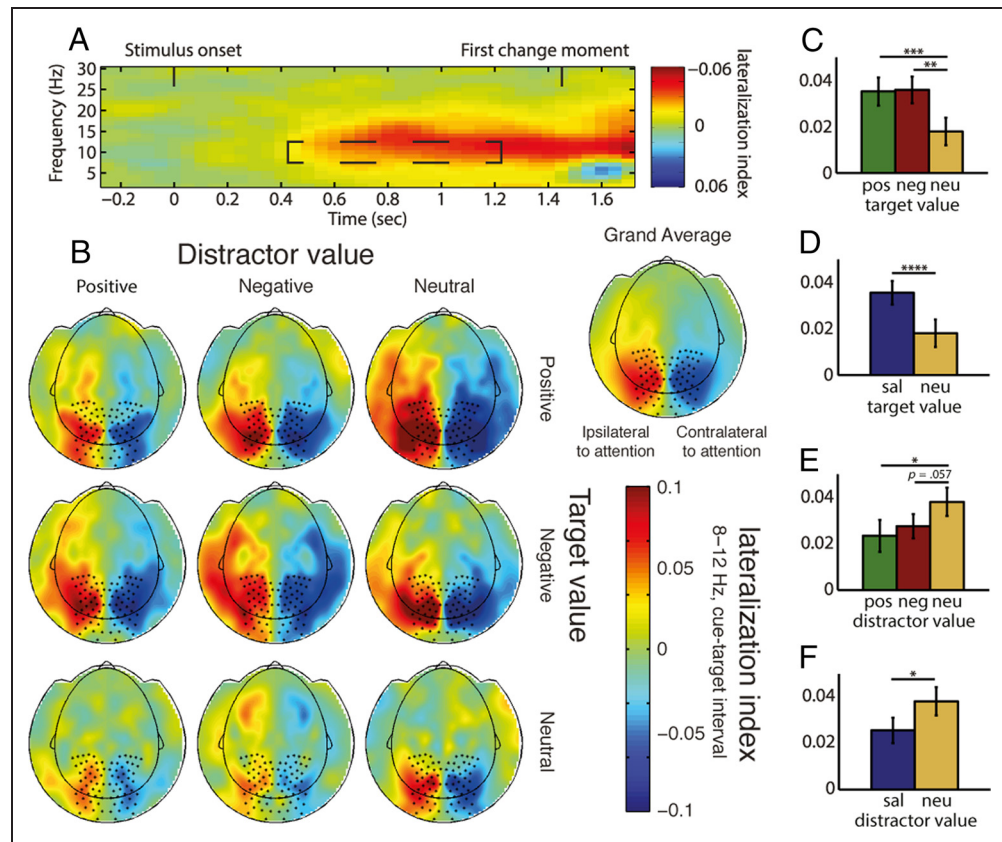
simultaneously with the spatial cue so that both the alpha and gamma would be modulated by attention and stimulation concurrently (Figure 1C). We concentrated our analysis in a 750-msec window locked to the cue. We quantified the lateralization of alpha power according to the formula

$$\text{ALI}_j = (\text{Power}_{j,\ \text{ipsilateral hemisphere}}$$
$$- \text{Power}_{j,\ \text{contralateral hemisphere}})/$$
$$\text{Power}_{j,\ \text{ipsilateral hemisphere}}$$
$$+ \text{Power}_{j,\ \text{contralateral hemisphere}}).$$

The contrast detection task with covert spatial attention produced robust attentional lateralization in the alpha band (8–12 Hz) in posterior sensors: When participants were cued to attend to a stimulus on the left, they showed low alpha power in the right hemisphere compared with the left hemisphere, and when cued to the right the reverse pattern was observed, consistent with many previous findings (Handel et al., 2011; Thut et al., 2006; Worden et al., 2000). Figure 2A shows the lateralization index for low frequencies averaged over all target and distractor value conditions calculated for the parieto-occipital sensors where the alpha lateralization effect was largest in the grand average (Figure 2B, "Grand Average"). Clear, band-limited activity is visible in the alpha band, beginning approximately 450 msec after stimulus onset and persisting until the period where the contrast change could occur.

We focused the subsequent analysis on the 450–1200 msec interval. Plotting the topographies of each value condition separately revealed clear differences in the magnitude of the lateralization as a function of the value of the stimuli (Figure 2B). Both target and distractor values appeared to influence the alpha lateralization, with alpha lateralization being strongest when targets were salient (positive or negative) and weakest when distractors were salient.

To quantify the above statistically, alpha-band (8–12 Hz) lateralization in the period between the cue and the contrast, change was computed for each value condition separately and entered into a 3×3 rmANOVA with factors Target value association (positive, negative, neutral) and Distractor value association (positive, negative, neutral). This revealed statistically significant main effects of Target value, $F(2, 50) = 7.85$, $p = .001$, and Distractor value, $F(2, 50) = 3.27$, $p = .046$, but no significant interaction, $F(4, 100) = 1.15$, $p = .34$.

To investigate the main effect of Target value association, data were averaged over distractor value association and compared using paired-samples t tests (Figure 2C). This revealed significantly higher alpha lateralization indices for both positive and negative targets compared with neutral targets: positive targets, $t(25) = 3.94$, $p = .0006$, and negative targets, $t(25) = 3.49$, $p = .0018$. Alpha lateralization indices for positive and negative targets did not differ from each other, $t(25) = 0.12$, $p = .91$. To directly test the hypothesis that alpha lateralization is sensitive

to the association of targets with salient outcomes, alpha lateralization indices for positive and negative targets were averaged together and compared with the neutral target alpha lateralization index in a paired-samples t test (Figure 2D). This revealed significantly greater values for value-salient targets, $t(25) = 4.63$, $p = .000097$. To compute effect size analysis of the target saliency effect, we calculated the square of Pearson's r according to the formula $r^2 = t^2/(t^2 + df)$: This revealed an r^2 of .46, indicating a large effect size (Cohen, 1988). Thus, alpha oscillations are biased according to the salience of targets.

Salient Distractors Decreased Alpha Lateralization

Similarly, to investigate the main effect of distractor, alpha lateralization index values were averaged with respect to target value and compared using paired-samples t tests (Figure 3E). This revealed significantly greater alpha lateralization index values for neutral distractors compared with positive distractors, $t(25) = 2.14$, $p = .043$, and showed a trend for being greater than that of negative distractors, $t(25) = 2.00$, $p = .057$. Positive and negative distractors did not differ from each other, $t(25) = 0.76$, $p = .46$. To test directly the hypothesis that alpha lateralization is sensitive to the association of distractors with salient outcomes, alpha lateralization indices for positive and negative distractors were averaged together and compared with that from neutral distractors in a paired-

samples t test (Figure 3F). This revealed significantly reduced alpha lateralization for value-salient distractors, $t(25) = -2.30$, $p = .03$. Effect size analysis of the distractor saliency effect revealed an r^2 of .18, indicating a medium effect size. Thus, alpha oscillations are biased by the salience of both targets and distractors, that is, irrespective of their relevance.

Gamma Lateralization Was Responsive to the Valence of Distractors

The visual stimuli and covert spatial attention also produced a modulation of the gamma lateralization index in the period between stimulus onset and contrast change, albeit weaker than the alpha modulation, again consistent with previous work that has shown gamma-band activity changing as a function of spatial attention (Koelewijn et al., 2013; Siegel et al., 2008). Figure 3A shows the lateralization index for high frequencies averaged over all target and distractor value conditions. Attentional lateralization is visible both before and after the contrast change moment. Plotting the topographies of each condition separately revealed a complex picture (Figure 3B). In some conditions—notably the "neutral target, negative distractor" condition, the pattern of lateralization seemed to be reversed compared with the grand average.

To statistically investigate these observed differences, gamma-band (45–65 Hz) lateralization during the period

Figure 3. Gamma lateralization demonstrates sensitivity to distractor valence but not to distractor salience or to target value. (A) Gamma attentional lateralization index, averaged across all conditions. Lateralized gamma-band activity is visible in the interval between stimulus onset and contrast change. (B) Topographies of attentional lateralization in the 45–65 Hz band for each value of target and distractor. (C, D) Target valence and target salience did not module attention-related gamma lateralization. (E) Negative distractors elicited significantly different levels of the gamma lateralization index compared with positive and neutral distractors. (F) Salient distractors (i.e., average of positive and negative) did not elicit a significantly different gamma lateralization index compared with neutral distractors. Error bars indicate standard errors of the mean. Asterisks denote statistical significance; *$p < .05$.
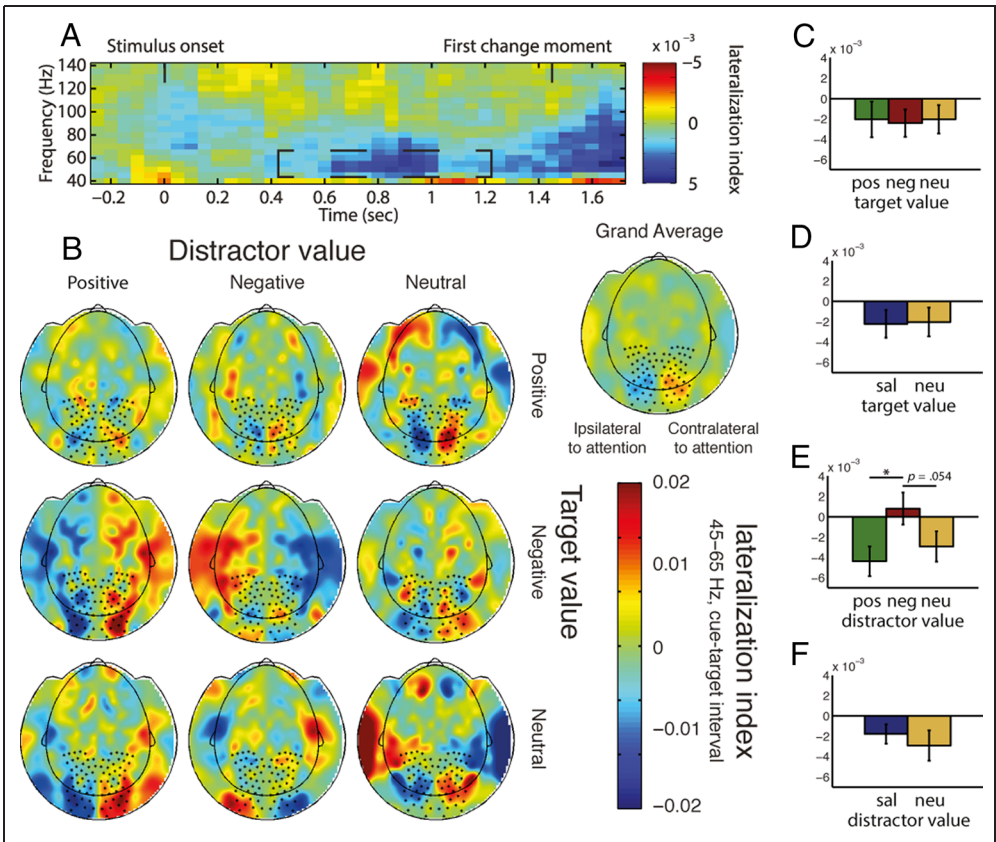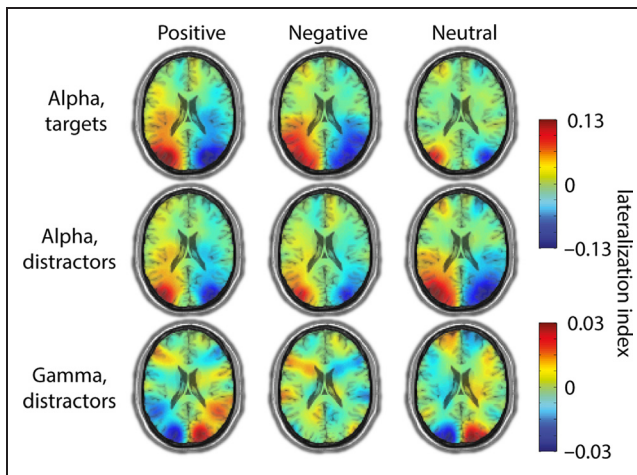
Figure 4. Statistical source maps of the main effects of target and distractor value on alpha and gamma lateralization indices from the time period between stimulus onset and contrast change, overlaid and projected into source space. All effects are clearly maximal in occipital cortex. Note that no effect of target value was observed in the gamma band.

between stimulus onset and contrast change was computed for each condition separately and entered into a 3×3 rmANOVA as for the alpha data. This revealed a statistically significant main effect of Distractor value, $F(2, 50) = 3.74$, $p = .031$, no significant main effect of Target value, $F(2, 50) = 0.023$, $p = .977$, and no significant interaction, $F(4, 100) = 1.21$, $p = .31$.

Although no significant main effect of target value was revealed by the rmANOVA, we nonetheless tested whether pairwise differences in gamma lateralization index were detectable as a function of target outcome-salience or valence, for consistency with the analysis of the alpha data. However, pairwise t tests revealed no significant differences ($t < 0.2$, $p > .9$ in all cases; Figure 3C, D).

To investigate the significant main effect of Distractor value, gamma lateralization indices were averaged with respect to target value and compared using paired-samples t tests (Figure 3E). In contrast to the alpha band, this analysis revealed significantly higher gamma lateralization indices for negative distractors compared with positive distractors, $t(25) = 2.21$, $p = .036$, and showed a trend as compared with neutral distractors, $t(25) = 2.02$, $p = .054$. Effect size analysis revealed r^2 values of .17 and .20, indicating medium effect sizes. Gamma lateralization index values from neutral distractors did not differ significantly from those of positive distractors, $t(25) = -0.904$, $p = .37$. Thus, gamma oscillations were biased in a valence- and relevance-specific manner; they were abolished only when a negative stimulus appeared in the distractor position.

Despite the opposing effects found for positive and negative distractors, for consistency with the analysis of the alpha-band data we tested the hypothesis that gamma lateralization is sensitive to the association of distractors with salient outcomes. Gamma lateralization index values

for positive and negative distractors were averaged together and compared with neutral distractors in a paired-samples t test (Figure 3F). This did not reveal a significant difference, $t(25) = 0.896$, $p = .38$.

Alpha and Gamma Effects Overlap in Occipital Cortex

To identify the location of the cortical sources underlying the observed effects of both voluntary attention and stimulus value on alpha and gamma lateralization, we used a beamforming approach (Figure 4). Consistent with our sensor analysis, attentional alpha lateralization was visible in all value conditions, but markedly stronger when targets had either positive or negative value and weaker when distractors had positive or negative value. To confirm that the observed alpha and gamma modulations were occipital, we identified the peak of maximum lateralization in each value condition and looked up the peak coordinate in the AAL atlas (Tzourio-Mazoyer et al., 2002; Table 1). For the alpha band, all conditions showed the strongest lateralization in the middle portion of the occipital cortex. For the gamma band, both "positive distractor" and "neutral" distractor conditions showed the strongest modulation in superior occipital cortex, with the "negative distractor" condition showing no lateralization in this region. (The actual peak did not correspond to an AAL-defined region and was in the vicinity of the cerebellum). This is evidence for occipital generation of the effects of value history and voluntary attention on

Table 1. MNI Coordinates of Maximal Lateralization of Oscillatory Power for the Different Reward Conditions

Condition	Peak Position (MNI)	Region (AAL Atlas)
Alpha		
Positive targets	[3.2 −8.8 1.6]	Middle occipital
Negative targets	[4.0 −8.8 1.6]	Middle occipital
Neutral targets	[4.0 −8.0 2.4]	Middle occipital
Positive distractors	[4.0 −8.8 1.6]	Middle occipital
Negative distractors	[4.0 −8.8 2.4]	Middle occipital
Neutral distractors	[3.2 −8.0 2.4]	Middle occipital
Gamma		
Positive distractors	[1.6 −8.8 1.6]	Superior occipital
Negative distractors	[4.0 −8.8 −3.2]	NA
Neutral distractors	[1.6 −9.6 2.4]	Superior occipital

As alpha lateralization is measure of interhemispheric differences in power, the sign of the X coordinate is irrelevant. "NA" indicates that the peak coordinate did not lie in a region defined by the AAL atlas (Tzourio-Mazoyer et al., 2002).

alpha and gamma oscillations and could indicate a common or overlapping source generator for these effects.

DISCUSSION

Our attentional system needs to perform a variety of competing tasks to optimize behavior; voluntary influences should allow us to focus on relevant information, but stimuli with important learned associations should be able to intrude on our awareness and "capture" processing resources even when not directly task relevant. Here, we found that two important indices of stimulus processing—alpha and gamma oscillations localized to occipital cortex—were dramatically influenced by the value associations of the stimuli, in some cases by as much as a factor of 2 (Figure 3D). Importantly, oscillations in these different frequency bands were biased in distinct ways according to the salience, valence, and relevance of the stimuli, suggesting that they may represent complementary mechanisms for processing stimulus–value associations.

First, alpha lateralization was influenced primarily by the association of the target and distractor stimuli with salient financial outcomes; targets associated with financially salient outcomes increased attentional orienting, primarily by further decreasing alpha power in target-processing regions (contralateral to attention), which is hypothesized to release those regions from inhibition (Jensen & Mazaheri, 2010). Correspondingly, distractors associated with salient financial outcomes decreased attentional alpha lateralization. Thus, in addition to its role in top–down attention (Thut et al., 2006; Worden et al., 2000), alpha oscillations appear to be important for gating information according to its acquired salience and irrespective of the current task relevance of the stimuli.

In contrast, lateralization of gamma-band activity—believed to represent active processing and support increased neuronal gain (Jensen, Kaiser, & Lachaux, 2007)—was influenced by the valence of the distractor. Distractors associated with losses caused a relative increase in gamma-band activity in distractor-processing regions (ipsilateral to attention), suggesting selective enhanced neural gain in the representation of the distractor stimulus when it was associated with a negative outcome. Gamma-band activity thus differentiates items on the basis of their valence—how positive or negative the stimuli are.

It has previously been shown that both visual alpha and gamma power may be manipulated by the valences of the stimuli in the visual field; viewing positive and negative images decreases posterior alpha power compared with neutral images (De Cesarei & Codispoti, 2011), whereas viewing unpleasant (compared with neutral) images increases posterior gamma power (Popov, Steffen, Weisz, Miller, & Rockstroh, 2012). Our study complements and extends these findings, demonstrating that stimulus–reward associations bias electrophysiological indices of attentional orienting even when these associations are entirely orthogonal to the current task. How-ever, although attention has been shown to produce task-specific, behaviorally relevant changes in the amplitude of both alpha and gamma oscillations (Koelewijn et al., 2013; Handel et al., 2011; Hoogenboom et al., 2010; Siegel et al., 2008; Thut et al., 2006; Fries et al., 2001), they most likely rely on different mechanisms (Bastos et al., 2015; Brunet et al., 2015), which may in turn explain why different reward associations differentially interacted with attentional alpha- and gamma-band lateralization.

The dissociation we observed of oscillatory frequency with stimulus feature may indicate that alpha and gamma are differentially controlled by two different mechanisms (Corbetta & Shulman, 2002). Several studies have indicated that the dorsal network provides top–down control of posterior alpha oscillations during selective attention (Marshall et al., 2015), and the intraparietal sulcus (IPS) may also be involved in the generation of the alpha rhythm (Thut et al., 2011; Tuladhar et al., 2007). Other evidence implicates the FEFs and IPS—key nodes in the dorsal network—in the representation of reward. Visual cues indicating rewards produce increased activations of bilateral IPS relative to unrewarding cues (Serences, 2008). Manipulation of dopamine receptors in FEF has also been shown to enhance selectivity and reliability of spike responses to a visual stimulus in V4 (Noudoost & Moore, 2011a). Our results are entirely commensurate with the notion that voluntary attention and stimulus salience exert their effects via common mechanisms (Stănişor et al., 2013). Indeed, we extend this concept by demonstrating that they share a common electrophysiological signature; when the target was salient—that is, when attention and salience were aligned—this produced a "super lateralization" in the alpha band, and when the distractor was salient—that is, when attention and salience were in conflict—this attenuated alpha lateralization.

It is interesting that gamma oscillations appear to be primarily sensitive to negative distractors. Task-irrelevant unpleasant background information has been shown to draw attention away from a visual detection task performed at fixation (Hindi Attar & Müller, 2012), and unpleasant faces have been shown to increase gamma-band activity during masked face detection (Luo et al., 2009). One possible explanation for the interaction of stimulus valence with stimulus task relevance may be a different contribution of the dorsal and ventral networks (Corbetta & Shulman, 2002) to alpha- and gamma-band activity. Engagement of goal-directed attention to a target may cause alpha power to decrease, "opening the gate" (Jensen & Mazaheri, 2010) and enabling processing of task-relevant information—for example, a contrast change—equally for all stimuli. Conversely, goal-directed attention requires the inhibition—"closing the gate"—of a distractor, potentially via an alpha power increase (Handel et al., 2011). However, when the distractor signals a financial loss, this may engage the ventral network, which is believed to act as a "circuit breaker" (Corbetta & Shulman, 2002). This would predict that the distractor would capture some

attentional resources, resulting in increased gamma-band activity and increased propagation (via greater neuronal gain) of this signal to higher-order regions. However, it remains an open question why correspondingly important information about a financial gain from a task-irrelevant stimulus did not exert a similar attentional capture as reflected in the gamma band. It is known that losses are felt more keenly than equivalent gains in certain circumstances (Novemsky & Kahneman, 2005); thus, it may be the case that a signal of an imminent loss captures more attention and is processed in a prioritized manner.

As well as considering the contribution of cortical attentional networks to the reward effects reported here, it is highly plausible that subcortical networks play a role. A body of evidence links the generation of the cortical alpha rhythm to the thalamus (Lopes da Silva, 1991), and the pulvinar has been shown to synchronize regions of cortex in the alpha range in response to changing attentional demands (Saalmann, Pinsk, Wang, Li, & Kastner, 2012). Thus, alpha oscillations may be a feature of long-range synchrony between cortical and subcortical regions. In contrast, visual stimulus-induced gamma-band activity is observed in visual cortex but not in LGN (Bastos, Briggs, Alitto, Mangun, & Usrey, 2014). Because subcortical structures contribute to the generation of the alpha rhythm whereas gamma activity emerges locally in the cortex, it may also be the case that BG substructures involved in reward and salience processing (Gurney, Prescott, & Redgrave, 2001) contribute differentially to the modulation of these rhythms with attention. Quantifying the respective influence of cortical and subcortical structures on the oscillatory lateralization effects reported here should be a major question for future research.

A further intriguing hypothesis concerns the role of neuromodulators in biasing attention. Although both dopamine and acetylcholine have been posited to play a role in attentional control (Noudoost & Moore, 2011a; Herrero et al., 2008), they may differentially contribute to bottom–up and top–down attention (Hasselmo & Sarter, 2011; Noudoost & Moore, 2011b), which depend on dissociable neural circuits (Buschman & Miller, 2007). Because gamma-band activity likely reflects a bottom–up drive to the visual system whereas alpha oscillations are likely under top–down control (Jensen, Bonnefond, Marshall, & Tiesinga, 2015), this would suggest dissociable effects of these two neuromodulators on the different frequency bands. Indeed, physostigmine—a cholinergic agonist—selectively enhances attentional modulation of alpha but does not affect stimulus-induced gamma band activity (Bauer et al., 2012). Perhaps dopaminergic manipulation would conversely alter attentional modulation of gamma activity while leaving alpha activity unaffected. The combination of MEG with pharmacological manipulations can provide useful insights in future studies (Muthukumaraswamy, 2014).

An important feature of this study is the orthogonalization of attention and motivation. Although our stimuli were associated with a positive or negative value before performance of the MEG task, participants were informed ahead of time that financial reward and penalty occurred irrespective of task performance. This reduces the possibility that participants simply made more effort to perform the task well on trials where a rewarding stimulus was present, because the reward would be received in any case. This may explain why simple response speed differences were not observed as a function of stimulus value. This contrasts with previous studies that may have confounded the relative contribution of attention and reward to the observed neural signals (Maunsell, 2004). Indeed, measuring the effect of financial outcome on attention directly—as we have done—has been shown to lead to very different behaviors compared with manipulating motivation and exerting consequent effects on attention (LePelley, Pearson, Griffiths, & Beesley, 2015).

In conclusion, two distinct signatures of expedited stimulus processing observed during voluntary attention—lateralization of occipital alpha- and gamma-band oscillatory activity—are both also altered as a function of value associations of stimuli in the visual field, even when those value associations are not task relevant. Alpha power alters when a stimulus is associated with a salient outcome, and gamma in distractor-processing regions is selectively boosted when a distractor is negative. Our findings provide important insights into the interaction between the behaviorally critical features of value and attention.

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