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Spatial Attention Enhances the Neural Representation of Invisible Signals Embedded in Noise

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This research was supported by the Australian Research Council (ARC) Centre of Excellence for Integrative Brain Function (ARC Grant CE140100007). J.B.M. was supported by an ARC Australian Laureate Fellowship (FL110100103). The authors declare no competing financial interests.

Abstract

Recent evidence suggests that voluntary spatial attention can modulate neural representations of visual stimuli that do not enter conscious awareness (i.e. invisible stimuli), supporting the notion that attention and awareness are dissociable processes (Watanabe et al., 2011; Wyart et al., 2012a). It remains unclear, however, whether spatial attention can modulate neural representations of invisible stimuli that are in direct competition with highly salient and visible stimuli. Here we developed a novel electroencephalography (EEG) frequency-tagging paradigm to obtain a continuous readout of neural activity associated with visible and invisible signals embedded in dynamic noise. Participants (*N* = 23) detected occasional contrast changes in one of two flickering image streams on either side of fixation. Each image stream contained a visible or invisible signal embedded in every second noise image, the visibility of which was titrated and checked using a two-interval forced-choice detection task. Steady-state visual-evoked potentials (SSVEPs) were computed from EEG data at the signal and noise frequencies of interest. Cluster-based permutation analyses revealed significant neural responses to both visible and invisible signals across posterior scalp electrodes. In line with previous findings, spatial attention increased the neural representation of visible signals. Crucially, spatial attention also increased the neural representation of invisible signals. As such, the present results replicate and extend previous studies by demonstrating that attention can modulate the neural representation of invisible signals that are in direct competition with highly salient masking stimuli.

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Significance Statement

There has been much debate about the extent to which attention can effect neural representations of stimuli that do not enter conscious awareness. It remains unclear, however, whether spatial attention can modulate representations of invisible stimuli that are in direct spatial and temporal competition with salient masking stimuli. We developed a novel paradigm that for the first time allowed us to measure weak neural representations of invisible stimuli embedded in spatially coincident noise, and tested the effect of spatial attention on these representations. We found that spatial attention enhanced the neural representation of invisible stimuli, demonstrating that competition with highly salient stimuli does not suppress the effects of spatial attention on weak neural representations of invisible stimuli.

Introduction

When viewing a cluttered visual scene, representations of the various objects compete for limited neural resources (Broadbent, 1958; Desimone and Duncan, 1995). Such ongoing neural competition can be biased by top-down mechanisms to facilitate the observer's behavioural goals (Beck and Kastner, 2009). For example, voluntarily allocating covert spatial attention to a specific region of the visual field can selectively boost neural representations of salient stimuli within that region (Hillyard and Anllo-Vento, 1998; Müller et al., 1998; Martinez et al., 1999). Recent evidence suggests that spatial attention can also enhance neural representations of weak stimuli that do not enter awareness (equated here with the contents of conscious experience; Schurger et al., 2008; Wyart and Tallon-Baudry, 2008; Watanabe et al., 2011; Wyart et al., 2012a). Since these attention effects occurred without a corresponding increase in object awareness, the above studies contradict the classic view that attention and awareness are identical processes (Prinz, 2012). Instead, attention and awareness are increasingly viewed as dissociable mechanisms (Koch and Tsuchiya, 2012; Tallon-Baudry, 2012), but the nature of their intricate relationship remains to be fully characterised. In particular, no study to date has investigated whether spatial attention can modulate neural representations of invisible signals that are in direct competition with visible stimuli, such as when signals are presented concurrently with, and at the same location as, highly salient masking noise. Such research is necessary if we are to understand how top-down mechanisms in the visual system allocate limited resources to competing stimuli with different levels of bottom-up signal strength (i.e. salience). Here we used electroencephalography (EEG) to determine whether voluntary covert

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spatial attention modulates neural representations of invisible stimuli embedded in highly salient noise.

To investigate this question, it is necessary to disambiguate relatively weak neural activity arising from subjectively invisible targets from the stronger responses associated with highly salient and spatially coincident masking stimuli. To date, however, no such technique has been devised to effectively distinguish the neural signatures of these weak and strong sensory inputs. If a train of stimuli is presented at a fixed frequency, however, a stable oscillatory response is produced in the brain that can be observed in the frequency-domain in EEG recordings (the steady-state visual-evoked potential; SSVEP; Regan, 1966). Multiple stimuli in a visual scene can thus be 'frequency tagged' when flickered at unique frequencies, an approach that has proven useful for exploring the effects of attention on visible stimuli at separate spatial locations (Norcia et al., 2015). This technique has recently been developed for frequency-tagging multiple stimuli at the *same* location (Ales et al., 2012), which could help address the question of whether spatial attention can modulate neural representations of invisible stimuli embedded in salient noise.

Here we developed a novel EEG frequency-tagging paradigm to obtain a continuous readout of neural activity associated with visible and invisible signals embedded in dynamic noise. Participants directed attention to one of a pair of flickering image streams to detect occasional contrast changes, and we assessed the effect of spatial attention on neural representations of both visible and invisible signals. We employed a two-interval, forced-choice signal detection task to confirm that appropriate levels of signal coherence were selected for visible and invisible signals. To anticipate, we found that spatial attention enhanced neural representations of both visible and invisible signals, suggesting that attention can bias neural activity in favour of invisible stimuli that are in spatial and temporal competition with highly salient masking noise.

Materials and Methods

Participants

Twenty-three healthy participants (11 female, mean age: 22.65 years) with normal or corrected-to-normal vision were recruited via an online research participation scheme at The University of Queensland. Participants completed a safety-screening questionnaire and provided written

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consent prior to commencement of the study, which was approved by The University of Queensland Human Research Ethics Committee.

Stimuli and apparatus

The method of stimulus generation (*Figure 1*) was adapted from Ales, Farzin, Rossion and Norcia (2012) to maintain the same average power distribution and luminance across all images. All images were created from the same seed image consisting of an annulus (seven cycles, inner diameter: 4.67° of visual angle, outer diameter: 14° of visual angle) on a uniform mid-grey square background (14° of visual angle). The phase distribution of the seed image was randomised separately for each image used in the experiment, and recombined with the original amplitude distribution to create a noise background. The annulus and noise background were then combined using complementary spatial blending masks (which spanned from the annulus edges to 2° of visual angle within each edge) to create an exemplar image consisting of a fully coherent annulus on a random noise background. Finally, the exemplar phase distribution was randomized according to the trial sequence (partially for a signal image; fully for a noise image), and recombined with the exemplar amplitude distribution. Phase angles of the exemplar were linearly interpolated in the direction of least difference to maintain a uniform phase distribution (for more information, see Ales, Farzin, & Norcia, 2012).

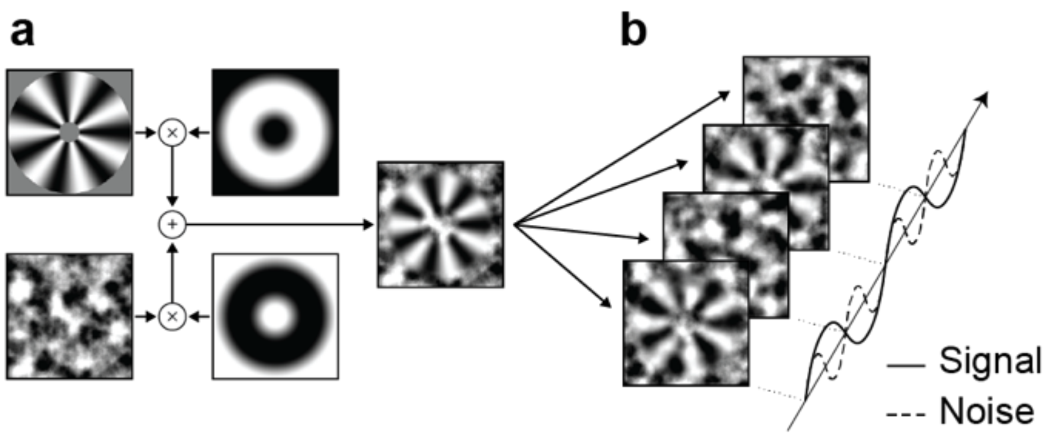

Figure 1. Stimulus generation and typical image sequence. (***A***) Phase distribution of the signal (annulus, top left) was scrambled to create a noise background that was different for every image (bottom left). Signal and noise images were combined via inverse masks to create an exemplar image (right), which was then phase-scrambled according to the desired level of signal coherence (i.e. *noise*, *invisible signal*, or *visible signal*). (***B***) Flickering images at a steady rate produced a neural response to the dynamic noise (which changed on every image) at the frequency of stimulation (10 or 15 Hz; the *noise SSVEP*). Crucially, signal (annulus) was embedded in every second image, which elicited a neural response at half the frequency of the noise SSVEP (i.e. 5 or 7.5 Hz; the *signal SSVEP*).

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Stimuli were presented on a 21-inch CRT monitor (NEC, Accusync 120) with a screen resolution of 800 x 600 pixels and a refresh rate of 120 Hz, using the Cogent 2000 Toolbox (http://www.vislab.ucl.ac.uk/cogent.php) for Matlab (The Mathworks Inc., Natick, USA) running under Windows XP. Participants were seated in a comfortable armchair in an electrically shielded laboratory, with the head supported by a chin rest at a viewing distance of 57cm.

Procedures

The present study used a within-participant design with two levels of target awareness (*visible*, *invisible*) and two levels of spatial attention (*attended, ignored*). Two tasks with similar overall designs were employed to manipulate awareness and spatial attention.

Awareness Task. Participants were presented with two square image streams on either side of fixation (visual angle: 14°), as illustrated in *Figure 2* and *Movie 1*. Each image stream contained two consecutive intervals that consisted of 0.5 *s* of static noise followed by 2.4 *s* of dynamic flickering noise. One of the two intervals in each stream (randomized separately) also contained signal (an annulus) embedded in every second noise image, the coherence of which increased linearly over the initial 0.4 *s* (to reduce involuntary capture of attention). Participants were asked to maintain fixation and report, on the cued side, which of the two intervals contained a signal (two-interval forced-choice), while ignoring the non-cued side. The cue direction (left or right) was randomized for the first trial of each block and then alternated every eight trials.

Participants completed two versions of the Awareness Task. The first version was run at the beginning of the experiment (following practice with accuracy feedback), in order to set signal coherence levels for the subsequent Attention Task (see below). In this first version, participants completed 48 trials with feedback, while levels of signal coherence were adjusted according to an adaptive Quest staircase (Watson & Pelli, 1983) designed to approximate the maximum level of signal coherence that could not be detected by each participant (i.e. the invisible condition). Signal coherence for the visible condition was then set 40% higher than this level, as guided by psychometric functions fitted to pilot data. The second version of the Awareness Task was run at the end of the experiment, to verify that appropriate levels of signal coherence had been selected. In this version, participants completed two blocks of 64 trials

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(without feedback) with each image stream containing visible *or* invisible signal in one of the two consecutive intervals (randomized separately across trials).

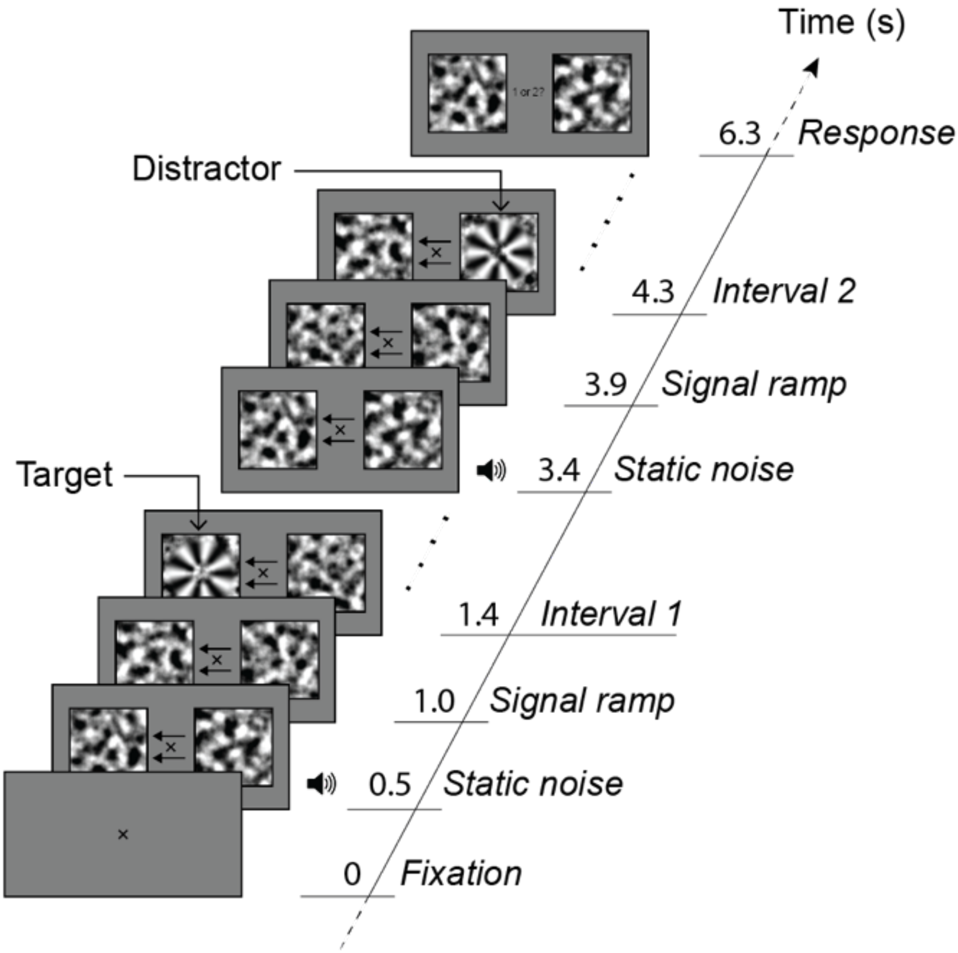

Figure 2. Awareness Task. Participants fixated centrally and searched for a signal embedded in dynamic noise on the cued side, which appeared in only one of two consecutive intervals. In the example shown, a target is present during interval 1 on the cued (left) side. Note that a distractor signal is also present during interval 2 on the ignored (right) side. Images flickered during the ramping and signal intervals only (see *Figure 1b* for typical image sequence).

Attention Task. Participants were again presented with two image streams on either side of fixation, which began flickering after 0.5 *s* of static noise (*Figure 3*; *Movie 2*). Unlike in the Awareness Task, however, only one flickering interval of 10.4 *s* duration was presented in each trial, and both image streams contained either a visible or an invisible signal (as per the staircase procedure above) embedded in every second noise image. Additionally, each image stream occasionally decreased in contrast before returning to normal across a 1 *s* period (ramping on and off linearly), with at least 1.5 *s* between peaks of contrast decreases (in either stream). Participants were asked to maintain fixation and report at the end of the trial how many contrast

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decreases (*targets*) occurred in the cued (*attended*) image stream. When the attended stream contained two contrast targets, the second target peaked between 7 *s* and 8.5 *s* into the trial, to encourage sustained attention throughout trials. Participants were allowed to practice the task (with feedback after each trial) before completing eight blocks of 64 test trials, with feedback provided between blocks. The percentage of contrast decrease was adjusted between blocks to maintain an approximate detection level of 65% (according to a 1 up 2 down staircase with step sizes of 5%).

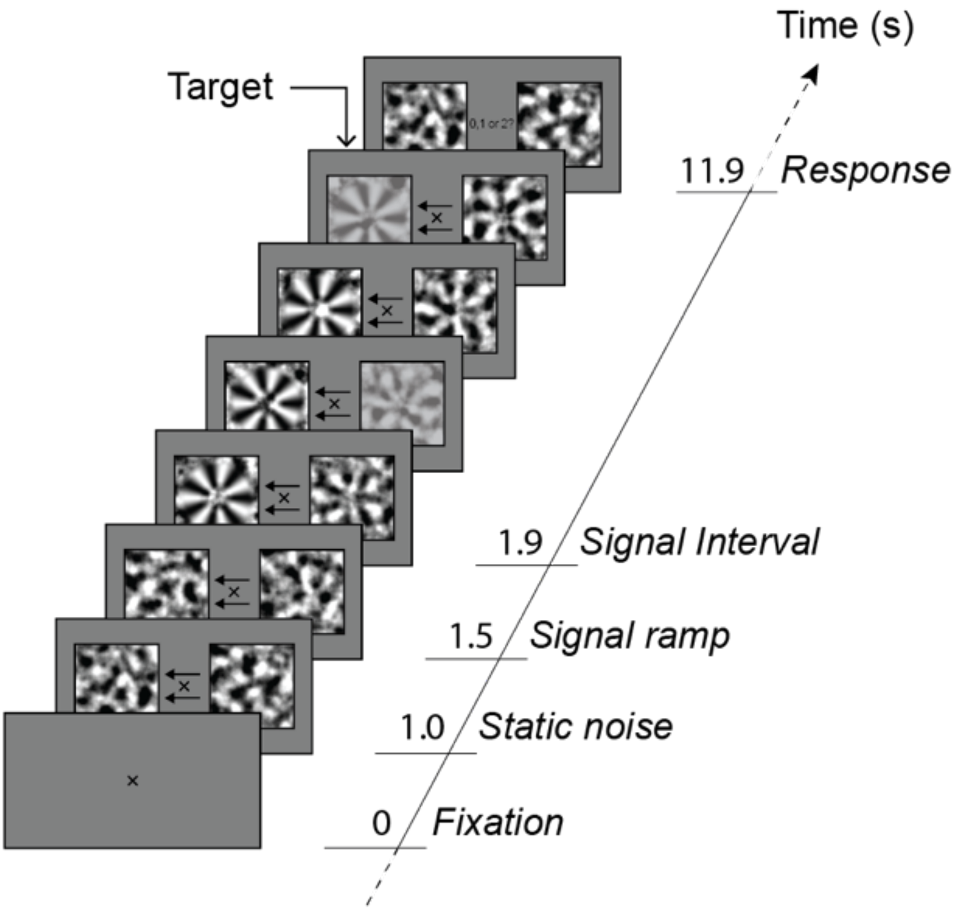

Figure 3. Attention Task. Participants fixated centrally and counted the number (0, 1 or 2) of brief decreases in contrast in the cued (attended) image stream. In the example shown, one contrast decrease appeared in each of the attended (left) and ignored (right) image streams. Each image stream contained a visible or invisible annulus embedded in dynamic noise throughout the entire signal interval. Note that for illustrative purposes the magnitude of the contrast decrements has been enhanced in the figure.

Stimulation frequencies. During both tasks, noise images in each image stream (i.e. attended and ignored) flickered at distinct frequencies (10 or 15 Hz, counterbalanced across trials), eliciting SSVEP responses at the frequency of noise stimulation (the *noise frequency*). Crucially, since signal (a partially scrambled annulus, as described above) was embedded in

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every second noise image (during signal intervals), a separate SSVEP was elicited at half the noise frequency in response to signal (5 or 7.5 Hz, the *signal frequency; Figure 1*). Thus we were able to isolate neural responses to both noise and signal (at two levels of awareness), when those stimuli were either attended or ignored (see Results for details of power computation).

EEG recording

Participants were fitted with a 64 Ag-AgCl electrode EEG system (BioSemi Active Two: Amsterdam, Netherlands) after the initial Awareness Task, and EEG data were recorded during the Attention Task and final Awareness Task. Continuous data were recorded using BioSemi ActiView software (http://www.biosemi.com), and were digitized at a sample rate of 1024 Hz with 24-bit A/D conversion and a .01 – 208 Hz amplifier band pass. All scalp channels were referenced to the standard BioSemi reference electrodes, and electrode offsets were adjusted to be below 25 μV before beginning the recording. Horizontal and vertical eye movements were recorded via pairs of BioSemi flat Ag-AgCl electro-oculographic electrodes placed to the outside of each eye, and above and below the left eye, and respectively.

EEG data pre-processing

Electroencephalography (EEG) recordings were processed offline using the Fieldtrip toolbox in Matlab (http://fieldtrip.fcdonders.nl). Trials containing horizontal eye movements were inspected manually and rejected if lateral eye fixations exceeded 1 *s* during the Attention Task (3.55% of trials) or 150ms during the final Awareness Task (12% of trials). Two faulty electrodes (across two participants) were interpolated using the nearest neighboring electrodes. Scalp electrode data were re-referenced to the average of all 64 electrodes, resampled to 256 Hz, and subjected to a surface Laplacian filter to control for volume conduction (Cohen, 2014). Trials were epoched into intervals containing signal at full coherence (Awareness Task: 1.4 – 3.4 *s* or 4.3 – 6.3 *s, Figure 2*; Attention Task: 1.9 *s* – 11.9 *s*, *Figure 3*), for frequency power analyses (see Results). Attention Task trials were also epoched with an additional 2 *s* before and after each signal period for time-frequency power analyses.

Results

Awareness Task

The initial adaptive staircase procedure produced an average signal coherence of 29.91% (SD: 3.18%) for the invisible condition and 69.91% (SD: 3.18%) for the visible condition. One-

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tailed t-tests were used to assess signal awareness in the final Awareness Task, which revealed that visible targets were detected well above chance level (50%; mean = 95.77%, SEM = .76, $t_{(22)} = 60.37$, $p < .001$) but below ceiling (100%; $t_{(22)} = -5.57$, $p < .001$), and detection of invisible targets was no better than chance (mean = 50.96%, SEM = 1.70, $t_{(22)} = .57$, $p = .289$). Furthermore, Bayesian statistics supported the null hypothesis that invisible stimuli were detected at chance (uniform prior, lower bound = 50%, upper bound = 100%, $B = .07$).

Attention Task

One-tailed t-tests revealed that contrast decrement targets were detected better than chance level (33%; mean = 66.69%, SEM = 1.34, $t_{(22)} = 49.50$, $p < .001$) but below ceiling level (100%; $t_{(22)} = -24.85$, $p < .001$). The behavioural results thus demonstrate that the Attention Task was sufficiently hard to require attention, without being too difficult.

Noise and Signal Elicit Distinct Neural Responses

To measure neural responses to the flickering stimuli during Attention Task epochs, we examined *phase-locked power* at each of the noise (10 and 15 Hz) and signal (5 and 7.5 Hz) stimulation frequencies, which was calculated as the difference between the *total power* and *non-phase-locked power* (for a detailed discussion, see Cohen, 2014). Total power was computed with Fourier transforms of individual epochs and averaged across trials within each condition (attention, awareness, stimulation frequency and side), and normalized to the average power (across all epochs) in the pre-stimulus period (0.2 – 1.0 *s*). Non-phase-locked power was calculated in the same manner as total power, after the condition-average event-related potential had been subtracted from each trial (Cohen, 2014). Phase-locked power was then calculated by subtracting the non-phase-locked power from the total power within conditions. *Figure 4* shows the phase-locked power (hereafter referred to as *power*) at electrode POz as a function of frequency, averaged across all Attention Task epochs. Note that power is only greater than zero at the signal (5 and 7.5 Hz) and noise (10 and 15 Hz) frequencies, confirming that the measure successfully isolated neural responses to the flickering stimuli.

For all subsequent analyses, we contralateralized electrodes in trials with right-sided stimulation (i.e., stimuli on the right of fixation flickered at the measured frequency), such that left-sided (right-sided) electrodes were those ipsilateral (contralateral) to stimulation. Since neither stimulation frequency or side were conditions of interest, we collapsed across these factors within levels of attention and awareness.

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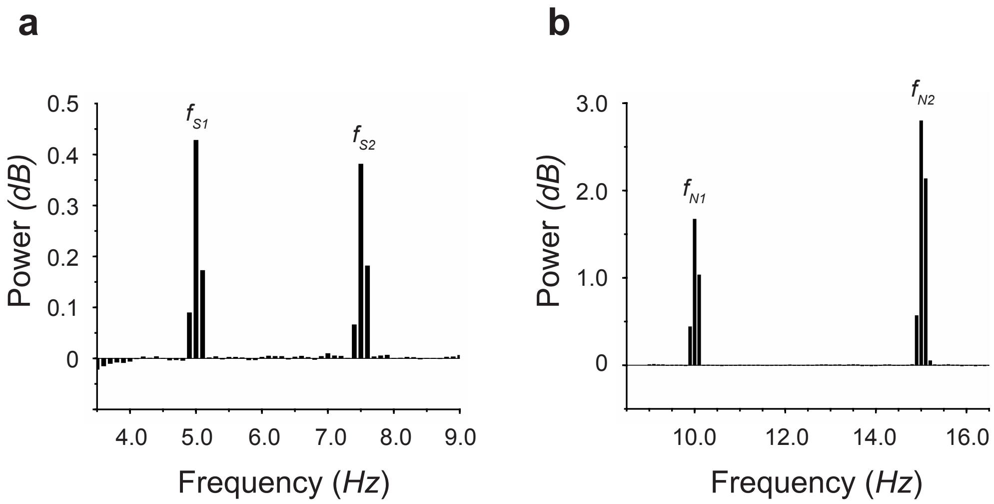

Figure 4. Phase-locked normalized power at electrode POz, averaged across all trials in the Attention Task. (*a*) Signal frequencies (5 and 7.5 Hz). (*b*) Noise frequencies (10 and 15 Hz).

Spatial Attention Enhances Neural Representations of Noise

To verify that attention was sustained covertly to the left or right side image stream across Attention Task epochs, we also calculated noise frequency power as a function of time. Preprocessed EEG data were bandpass filtered at each frequency of interest (width: .2 Hz, order: 64 samples, Matlab function: fir1), subjected to a Hilbert transform, and down-sampled to 40 Hz. Time-frequency power was then calculated as per phase-locked power (above), with the exception that a shorter baseline period was used to account for reduced temporal precision following Hilbert transforms (.3 to .7 *s*). Power was collapsed across awareness conditions (since all stimuli contained noise) and subjected to a one-tailed Monte-Carlo permutation test in *Fieldtrip* (between participant factors: electrode power and time, cluster $p < .05$, unit $p < .05$, 1000 permutations; for a detailed discussion, see Maris & Oostenveld, 2007). As revealed in *Figure 5*, spatial attention enhanced noise frequency power across a cluster of posterior and contralateral electrodes that spanned the entire epoch (Monte-Carlo $t = 13110$, $p < .001$, corrected for multiple comparisons in space and time).

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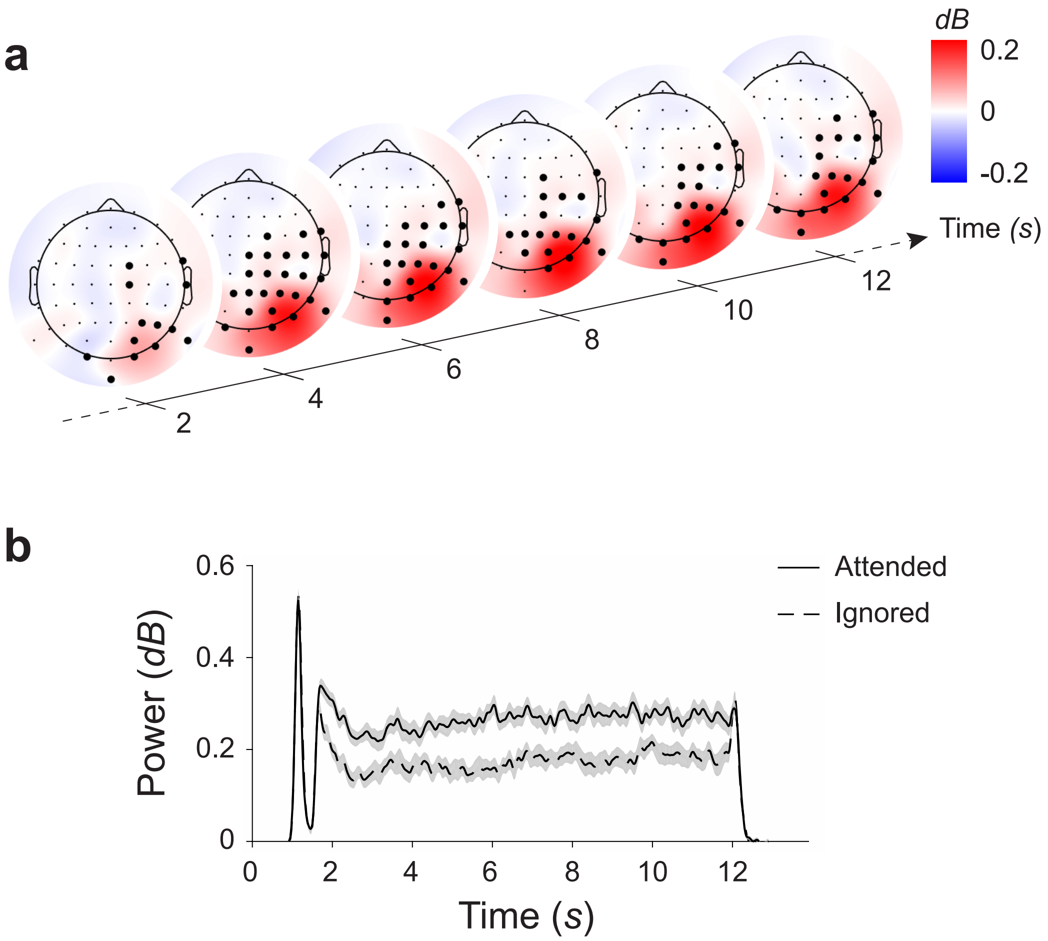

Figure 5. Effect of spatial attention on the neural response to noise in the Attention Task. (***a***) Electrode topographies represent the difference between attended and ignored noise SSVEPs, contralateralized to represent left side stimulation, and collapsed across noise frequencies (10 and 15 Hz). Larger dots indicate the cluster of electrodes that showed significantly greater noise frequency power with attention over time (cluster-based permutation test, Monte-Carlo $p < .001$). (***b***) Phase-locked normalised power averaged across contralateral electrodes P1/P2, PO3/PO4, and PO7/PO8. Shaded regions indicate the standard error of the mean (within-subjects).

Target Detection Correlates with Neural Representations of Noise

To investigate the relationship between neural representations of noise stimuli and behavioural performance on the Attention Task, we calculated noise frequency power (as above) after balancing the number of each participant's correct and incorrect trials within each combination of noise frequency and side (in the attended image stream only, since ignored stimuli were not responded to). Power during correct and incorrect trials was then subjected to a two-tailed Monte-Carlo permutation test (between participant factor: electrode power, cluster $p < .05$, unit $p < .05$, 1000 permutations). As can be seen in *Figure 6,* there was a larger neural response to noise stimuli across frontal and central electrodes when targets (contrast decrements) were correctly detected (Monte-Carlo $t = 28.34$, $p < .001$, corrected for multiple comparisons in

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space). This finding suggests that more reliable allocation of attention to the cued image stream (indexed by enhanced responses to noise stimuli) resulted in improved detection of targets. Additionally, the finding that target detection was associated with greater neural responses to noise at frontal and central electrodes, rather than posterior electrodes, might indicate greater involvement of frontal control mechanisms in the process of target detection (Ridderinkhof, 2004), or that target detection depended on forward propagation of neural responses to anterior regions of the visual cortex.

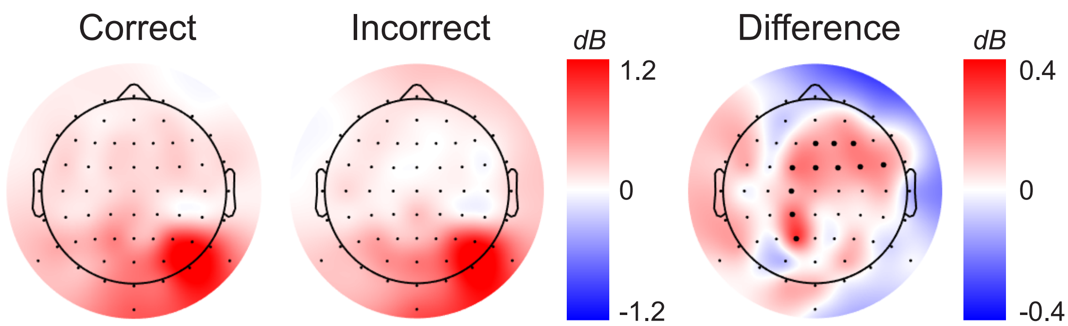

Figure 6. Relationship between target detection and the neural response to noise in the Attention Task. Electrode topographies are contralateralized to represent left side stimulation, and collapsed across noise frequencies (10 and 15 Hz). Larger dots indicate the cluster of electrodes with significantly greater power on correct trials than incorrect trials (cluster-based permutation test, Monte-Carlo $p < .001$).

Invisible Signals Elicit Reliable Frequency Responses

A central goal of our study was to demonstrate that invisible (and visible) signals elicit reliable SSVEPs. To do this we calculated power at the signal frequencies (5 and 7.5 Hz) and collapsed across frequencies, contralateralized sides, and attention conditions. We then compared the electrode distributions to a zero power electrode distribution with a one-tailed Monte-Carlo permutation test in *Fieldtrip* (between participant factor: electrode power, cluster $p < .05$, unit $p < .05$, 1000 permutations) (Maris and Oostenveld, 2007), separately for each level of awareness. As revealed in *Figure 7*, signal frequency power during presentation of a visible signal was significantly greater than zero across a broad posterior and mostly contralateral cluster of electrodes (Monte-Carlo $t = 115.67$, $p < .001$, corrected for multiple comparisons in space), confirming the presence of a neural response to visible signals. Crucially, signal frequency power during presentation of invisible signals was also significantly greater than zero across a cluster of posterior and mostly contralateral electrodes (Monte-Carlo $t = 17.51$, p

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= .009, corrected for multiple comparisons in space), confirming the presence of a neural response to invisible signals.

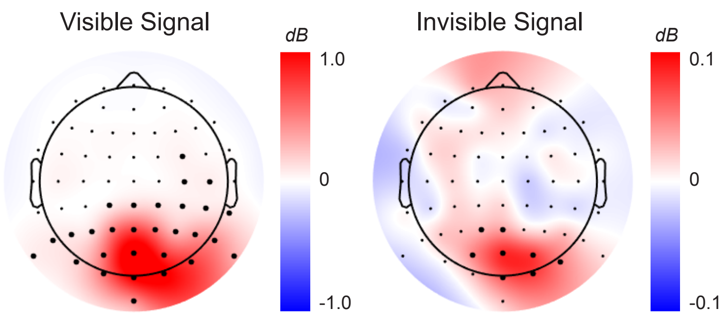

Figure 7. Neural response to visible and invisible signals in the Attention Task. Electrode topographies represent SSVEP power in response to visible signals (left) and invisible signals (right), contralateralized to represent left side stimulation, and collapsed across attention conditions and signal frequencies (5 and 7.5 Hz). Larger dots indicate clusters of electrodes with significant signal relative to a zero power topography map (cluster-based permutation test, Monte-Carlo $p < .05$).

Signal Frequency Responses Are Not Driven by Noise Stimuli

As a control, we checked whether the neural activity observed at signal frequencies might reflect a neural response to noise stimuli at half the frequency of stimulation. To do this we computed signal frequency power during intervals in the Awareness Task that contained only noise (i.e., without signal embedded in the contralateral image stream of interest). We normalised interval power to adjacent frequency bands (+/- 0.5, 1.0, and 1.5 Hz), since the pre-stimulus period was too brief to use as a baseline. Intervals containing only noise (at the signal frequency of interest) were collapsed across the cluster of electrodes showing a significant response to invisible stimuli in the Attention Task (Pz, POz, Oz, PO3, PO4, contralateral PO7/PO8, contralateral O1/O2, and ipsilateral P1/P2; see *Figure 7*). A one-tailed t-test demonstrated that signal frequency power during noise stimulation in the Awareness Task was not significantly greater than zero (mean < .01 *dB*, $p = .465$). Bayesian statistics supported the null hypothesis that noise stimuli produced no neural response at signal frequencies (uniform prior, lower bound = 0, upper bound = .06 *dB*, $B = .17$). Together, these results confirm that the observed neural activity at signal frequencies in the Attention Task was driven by signal stimuli.

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Attention Enhances Neural Representations of Visible and Invisible Signals

Considering the weaker neural response to signals compared with high-contrast noise (*Figure 4*), we collapsed power across posterior and contralateral clusters of electrodes that showed a significant response to the signal (*Figure 7*), separately for each level of awareness and attention. As revealed in *Figure 8*, attention increased the neural response to both visible and invisible signals across these electrode clusters. A two-way analysis of variance tested the effects of signal awareness (two levels: *visible*, *invisible*) and spatial attention (two levels: *attended, ignored*) on neural responses to signal. Results of the ANOVA revealed a main effect of signal awareness ($F_{(1,22)} = 46.457$, $p < .001$, $\eta_p^2 = .68$), with greater neural responses to visible signals (.37 *dB*) than to invisible signals (0.06 *dB*). Spatial attention also increased neural responses to stimuli ($F_{(1,22)} = 7.600$, $p = .012$, $\eta_p^2 = .26$), with significantly greater signal frequency power in response to attended signals (0.25 *dB*) than ignored signals (0.18 *dB*). The interaction between signal awareness and spatial attention was also significant ($F_{(1,22)} = 4.780$, $p = .040$, $\eta_p^2 = .18$).

Follow-up two-tailed t-tests assessed the simple main effects of spatial attention at each level of signal awareness (*Figure 8b*). Spatial attention modulated neural responses to visible signals, with greater activation in response to attended (mean = .43 *dB*) than ignored visible stimuli (mean = .31 *dB*, within-participants SEM = .03, $t_{(22)} = 2.69$, $p = .013$) This finding is in line with previous research showing attentional enhancement of SSVEPs to visible flickering stimuli (Vialatte, Maurice, Dauwels, & Cichocki, 2010). Crucially, spatial attention also modulated neural responses to invisible signals, with significantly greater activation in response to attended (mean = .08 *dB*) than to ignored invisible stimuli (mean = .04 *dB*, within-participants SEM = .01, $t_{(22)} = 2.08$, $p = .049$), indicating that attention can also enhance neural responses to invisible stimuli embedded in highly salient noise.

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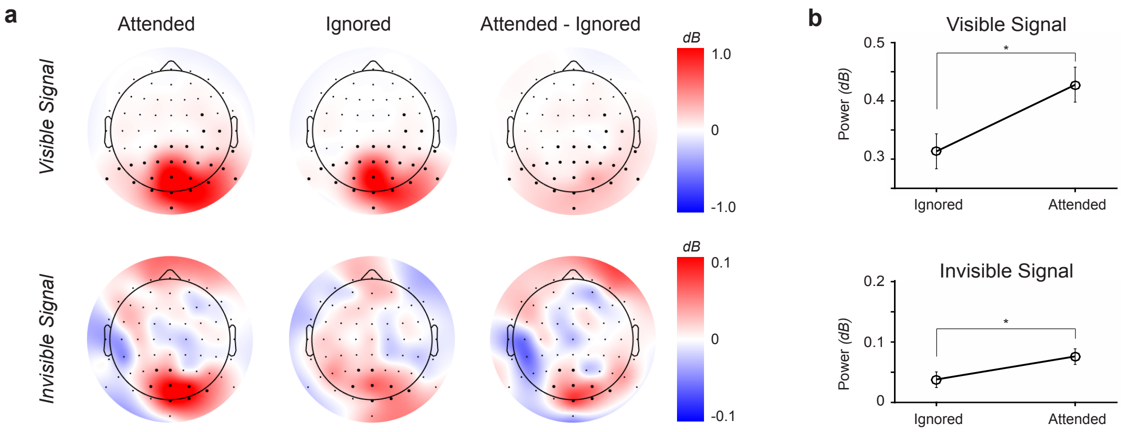

Figure 8. Effect of attention on neural responses to visible (top) and invisible (bottom) signals in the Attention Task. (***a***) Electrode power topographies for attended signals (left), ignored signals (middle), and the difference between attended and ignored signals (right). Topographies are contralateralized to represent left side stimulation, and collapsed across signal frequencies (5 and 7.5 Hz) Larger dots indicate electrodes showing significant signal (*Figure 7*), across which power was collapsed to investigate the effect of attention. (***b***) Effect of attention within each level of awareness, collapsed across electrodes showing significant signal. Attention significantly increased the neural response to both visible and invisible signals ($p < .05$).

Discussion

Previous research has suggested that covert spatial attention can modulate neural responses to invisible stimuli, supporting the notion that attention and awareness are dissociable neural processes (Wyart and Tallon-Baudry, 2008; Watanabe et al., 2011; Wyart et al., 2012a). Nevertheless, the intricacies of such a relationship remain poorly understood, such as whether covert spatial attention can modulate neural representations of invisible stimuli that are in spatial competition with highly salient noise. To investigate this question, we developed a novel attention task in which participants counted the number of brief contrast decreases in one of two image streams that contained both signals (visible or invisible) and noise. We isolated neural responses to noise in cued (attended) and non-cued (ignored) image streams, and observed enhanced activity across contralateral and posterior electrodes to cued noise throughout the trial epoch, confirming that participants voluntarily held their attention to one of the two lateralized image streams as instructed. Neural responses to noise were also enhanced across central electrodes with correct identification of contrast targets, suggesting that fluctuations in attention across trials directly affected target detection.

We employed a novel frequency tagging approach that allowed us to isolate neural responses to visible and invisible signals embedded in highly salient noise. To our knowledge, this is the first study to report SSVEP responses to invisible stimuli. This finding indicates that awareness

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of a stimulus is not a prerequisite for eliciting an SSVEP, as might be inferred from the step-like rise in SSVEP power that coincided with the onset of signal awareness in a previous study (Ales et al., 2012). Instead, our findings demonstrate that SSVEPs track intermediate levels of signal strength, even at levels too weak to provoke conscious perception.

Critically, our paradigm allowed us to measure the effects of spatial attention on neural responses to visible and invisible signals. We found that neural responses to visible signals were greater in the attended image stream than in the ignored stream, extending previous findings of enhanced neural responses to attended visible stimuli (Hillyard and Anllo-Vento, 1998; Müller et al., 1998; Martinez et al., 1999) to demonstrate that spatial attention also benefits partially degraded, yet still visible, signals in spatial competition with clearly visible and highly salient noise. Crucially, neural responses to invisible signals were also greater in the attended image stream than in the ignored stream, demonstrating that spatial attention enhances representations of invisible stimuli in direct spatial competition with highly salient and visible noise. Since spatial attention enhanced neural representations of signals without a corresponding increase in signal awareness, the present findings support the notion that spatial attention and awareness are dissociable neural mechanisms (Dehaene et al., 2006; Cohen et al., 2012; Koch and Tsuchiya, 2012; Tallon-Baudry, 2012).

Although the present study is not the first to demonstrate effects of spatial attention in the absence of object awareness (Schurger et al., 2008; Wyart and Tallon-Baudry, 2008; Watanabe et al., 2011; Wyart et al., 2012a), it makes several important advances on the existing literature. First, previous studies have not demonstrated that the observed neural activity, modulated by attention, was specifically related to the invisible stimuli in question. As such, the observed effects of attention may instead reflect enhanced neural representations of other, visible stimuli (such as the spatial cue in Wyart et al., 2012a), as has been argued elsewhere (Cohen et al., 2012). Alternatively, previously reported effects may have reflected subcomponents of spatial attention that do not modulate neural representations *per se* (for a review on the various subcomponents of attention, see Womelsdorf and Everling, 2015). For example, the effects observed in studies using probabilistic cues (Schurger et al., 2008; Wyart and Tallon-Baudry, 2008; Wyart et al., 2012b) could reflect re-orienting of attention after a miscued stimulus. Consistent with this interpretation, two such studies reported late effects of spatial attention (350 – 500 ms; Schurger et al., 2008; Wyart and Tallon-Baudry, 2008) that seem inconsistent with the earlier effects reported elsewhere (beginning at 100 ms post-stimulus; Eimer, 1995).

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In addition, previously observed effects of spatial attention could reflect baseline shifts in neuronal activity that occur even in the absence of external driving stimuli (Driver and Frith, 2000), as opposed to modulation of neural representations of invisible stimuli *per se*. In demonstrating that spatial attention modulates specific neural correlates of invisible stimuli, without a corresponding increase in awareness, the present study provides the first clear evidence that spatial attention and awareness dissociate at the level of neuronal representations.

Second, previous studies have presented signals at detection threshold and used participants' subjective reports to categorise trials according to visibility (e.g. Wyart et al., 2012a). In such paradigms, invisible signals are presented at the same intensity as visible signals (i.e. with enough bottom-up strength that they have the potential to enter awareness) and thus it remains possible that surpassing some minimum 'threshold' of activation might be required for neural representations to elicit effects of spatial attention. In contrast, we presented visible and invisible signals at different, pre-determined levels of coherence, and verified that invisible stimuli were objectively undetectable with a two-interval forced-choice signal detection task. Thus, we can be confident that invisible signals in our experiment were weaker than any hypothetical 'threshold' required for them to enter awareness, and that surpassing such a threshold is not a necessary requirement for neural representations to be affected by spatial attention. It could be argued that since we did not measure signal awareness during the Attention Task, participants might have been aware of the 'invisible' signal. Although we cannot rule this out, we argue that such a scenario is unlikely, considering that participants actively searched for signals in the Awareness Task, but looked instead for contrast decrements during the Attention Task.

A third, and arguably most important, advance of the current study is that we have shown that spatial attention can enhance neural representations of invisible stimuli that are in direct spatial competition with highly salient, visible stimuli. Previous studies presented invisible signals alone (Schurger et al., 2008; Wyart and Tallon-Baudry, 2008), or at different times or locations (Watanabe et al., 2011; Wyart et al., 2012a) to the salient masks used to titrate signal awareness. Since neural competition is maximal at the level of the receptive field (Reynolds et al., 1999; Beck and Kastner, 2009), neural representations of invisible signals in these studies were likely under conditions of minimal competition. In contrast, we maximised competition between signal and noise by presenting them concurrently and at the same location. Our findings reveal concurrent neural representations of both visible and invisible stimuli at the same location,

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demonstrating that spatial competition with highly salient stimuli is not sufficient to suppress weak neural representations of invisible stimuli. Moreover, the present study demonstrates that weak neural representations of invisible stimuli in competition with salient stimuli can nevertheless be biased according to the top-down goals of the observer – in this case, holding covert attention preferentially to the left or right visual field. Given that signal features were irrelevant to the contrast detection task, this finding suggests that all stimuli within the 'spotlight' of spatial attention are prioritised relative to those at unattended locations (Posner, 1980), irrespective of their task-relevance, their capacity to enter awareness, or their proximity to more salient stimuli.

Although previous studies have generally found that SSVEPs originate in primary visual cortex, other studies have localized sources of low-frequency SSVEPs to medial frontal cortices and even subcortical areas (Norcia et al., 2015). We observed posterior and contralateral patterns of scalp activity in response to the signal, consistent with sources in retinotopically organized primary visual cortex (Sereno et al., 1995; Engel et al., 1997). Thus, our findings suggest that attention modulates neural responses to invisible stimuli in early visual cortex. Whether attention can also modulate neural responses to invisible stimuli in hierarchically lower (subcortical) or higher (medial frontal) visual areas is beyond the scope of the present study, but remains an important question for future research.

The present findings demonstrate that spatial attention can operate independent of mechanisms of awareness, at the level of neural representations. More broadly, the present findings place spatial attention within a growing body of literature that suggests various forms of attention (e.g., temporal, feature-based, and involuntary spatial attention) can operate in the absence of stimulus awareness (for a review, see Koch and Tsuchiya, 2007). Together, these findings argue against the idea that attention and awareness are identical (Prinz, 2012) and instead support theories that cast attention and awareness as dissociable mechanisms (Dehaene et al., 2006; Cohen et al., 2012; Koch and Tsuchiya, 2012; Tallon-Baudry, 2012). Nevertheless, the exact nature of this relationship remains to be fully characterized, in particular whether the different forms of attention interact with awareness according to the same underlying principles, and how such top-down biases interact with bottom-up processes related to salience and neural competition between representations. To this end, we anticipate that the present paradigm could be adapted to study how other non-spatial forms of attention (e.g., feature-

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based) modulate neural representations of multiple competing stimuli at different levels of awareness.

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Supplemental Media

Movie 1. Example trial of the Awareness Task. At the beginning of the trial, static noise images appear on either side of fixation, and central arrows indicate the image stream to be attended (in this example, the left stream). After 0.5 *s* the image streams flicker for the first 2.4 *s* interval, are static for another 0.5 *s*, and then flicker again for the second 2.4 *s* interval. On the cued (left) side, one of the two flickering intervals contains signal embedded in every second image (in this example, the second interval), the coherence of which increases linearly during the first 0.4 *s* of the interval. Signal is also present in one of the two intervals on the non-cued (right) side (in this example, the first interval).

Movie 2. Example trial of the Attention Task. At the beginning of the trial, static noise images appear on either side of fixation, and central arrows indicate the image stream to be attended (in this example, the left stream). After 0.5 *s* the image streams flicker for 10.4 *s*. At the end of the trial participants report how many times the cued (left) image stream decreased in contrast (in this example, twice). The non-cued image stream also contains up to two contrast decrements (two in this example). Both image streams contain signal embedded in every second image, the coherence of which increases linearly during the first 0.4 *s* of flicker to a level that is either visible or invisible to the participant (in this example, the left image stream contains visible signal and the right image stream contains invisible signal).