

## Spatial attention improves reliability of fMRI retinotopic mapping signals in occipital and parietal cortex

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### ABSTRACT

Spatial attention improves visual perception and increases the amplitude of neural responses in visual cortex. In addition, spatial attention tasks and fMRI have been used to discover topographic visual field representations in regions outside visual cortex. We therefore hypothesized that requiring subjects to attend to a retinotopic mapping stimulus would facilitate the characterization of visual field representations in a number of cortical areas. In our study, subjects attended either a central fixation point or a wedge-shaped stimulus that rotated about the fixation point. Response reliability was assessed by computing coherence between the fMRI time series and a sinusoid with the same frequency as the rotating wedge stimulus. When subjects attended to the rotating wedge instead of ignoring it, the reliability of retinotopic mapping signals increased by approximately 50% in early visual cortical areas (V1, V2, V3, V3A/B, V4) and ventral occipital cortex (VO1) and by approximately 75% in lateral occipital (LO1, LO2) and posterior parietal (IPSO, IPS1, IPS2) cortical areas. Additionally, one 5-min run of retinotopic mapping in the attention-to-wedge condition produced responses as reliable as the average of three to five (early visual cortex) or more than five (lateral occipital, ventral occipital, and posterior parietal cortex) attention-to-fixation runs. These results demonstrate that allocating attention to the retinotopic mapping stimulus substantially reduces the amount of scanning time needed to determine the visual field representations in occipital and parietal topographic cortical areas. Attention significantly increased response reliability in every cortical area we examined and may therefore be a general mechanism for improving the fidelity of neural representations of sensory stimuli at multiple levels of the cortical processing hierarchy.

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### Introduction

In many human cerebral cortical areas, there is a one-to-one mapping between points in visual space and corresponding cortical locations, and locations in the visual field are represented as a topographic map on the cortical surface of these areas. The advent of functional magnetic resonance imaging (fMRI) has greatly facilitated the study of topographic organization in the human brain (Silver and Kastner, 2009; Wandell et al., 2007). Presentation of a stimulus that traverses the visual field generates traveling waves of activity in many topographically-organized areas. Retinotopic mapping refers to the process of characterizing topographic organization by identifying the visual field locations represented by each of a set of cortical locations and then determining the spatial patterns of these visual field representations on the cortical surface. The ability to objectively define topographic

cortical areas in individual subjects yields significant advantages for the study of cortical functional specialization. This provides motivation for developing methods to allow more efficient identification of the boundaries of topographic cortical areas and characterization of visual field representations in these areas.

There is substantial evidence to suggest that visual attention should improve the reliability of fMRI retinotopic mapping signals. Psychological research has established that allocation of attention to a location in visual space improves processing of stimuli at that location. Specifically, directing covert attention to a peripheral location decreases reaction time (Posner et al., 1980) and enhances accuracy (Bashinski and Bacharach, 1980) for detecting targets at the attended location. Additionally, electrophysiological studies in monkeys have demonstrated neural correlates of the enhancement of visual perception by spatial attention. When a visual stimulus is presented at an attended location, the amplitude of the neural response in many occipital and parietal cortical areas is greater than the response to the same stimulus when it is not attended (Bushnell et al., 1981; McAdams and Maunsell, 1999; Motter, 1993; Treue and Maunsell, 1996). Similar results have been obtained for human early visual cortical areas in fMRI experiments;

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directing attention to a visual location increases fMRI responses in portions of the visual field maps representing the attended location (Gandhi et al., 1999; Somers et al., 1999), even in the absence of visual stimulation (Kastner et al., 1999; Silver et al., 2007). Finally, recent studies report that in addition to increasing firing rate, attention also enhances the reliability of visual responses in monkey V4 neurons (Cohen and Maunsell, 2009; Mitchell et al., 2007; Mitchell et al., 2009).

Further evidence that spatial attention could enhance retinotopic mapping responses comes from the discovery of topographic maps of visual spatial attention signals in regions outside of visual cortex. IPS1 and IPS2 are regions in posterior parietal cortex that, like early visual cortical areas, contain a topographic map of the contralateral visual field (Silver et al., 2005). Unlike early visual cortex, IPS1 and IPS2 respond poorly to visual stimulation in the absence of attentional demands (Silver et al., 2005). In addition, allocation of attention to a rotating wedge stimulus containing point-light biological motion figures revealed topographic organization of fMRI responses in numerous areas, including lateral and ventral temporal cortex, superior temporal sulcus, parietal cortex, frontal eye fields, precentral sulcus, V6, and precuneus (Saygin and Sereno, 2008). Responses to the rotating wedge in these areas were reduced when subjects performed a difficult task at central fixation (Saygin and Sereno, 2008).

Although the evidence summarized above suggests that spatial attention would improve the quality of fMRI topographic mapping signals, many studies have employed passive viewing or a central fixation task during retinotopic mapping experiments. In this paper, we present the first quantitative analysis of the benefits of a spatial attention task for retinotopic mapping studies. Subjects viewed a rotating wedge stimulus that periodically traversed the visual field. On half of the fMRI runs, they continuously directed attention to the wedge stimulus and performed a target detection task within the wedge. On the other half, subjects performed an equally challenging target detection task within the fixation point. When attention was directed to the retinotopic mapping stimulus instead of the central fixation point, the signal-to-noise ratio (SNR), or reliability, of the fMRI retinotopic mapping signals increased. This increase in SNR was observed in early visual (V1, V2, V3, V3A/B, V4), lateral occipital (LO1 and LO2; Larsson and Heeger, 2006), and ventral occipital (VO1; Brewer et al., 2005) cortical areas, as well as in posterior parietal areas that contain topographic maps of spatial attention (IPSO (also known as V7; Tootell et al., 1998) and IPS1 and IPS2 (Silver et al., 2005)). The benefits of attending to the retinotopic mapping stimulus may be particularly important for investigators who seek to establish topographic maps with as little scanning time as possible, leaving more time for other research questions. Finally, the increase in response reliability due to attending the retinotopic mapping stimulus was observed in all identified cortical areas, spanning multiple levels of the visual processing hierarchy. This finding suggests that there may be a general mechanism by which allocation of attention to a stimulus enhances the reliability of its representation in the cerebral cortex.

## Materials and methods

### Subjects

Eight healthy subjects participated in the study, all of whom had extensive experience as participants in psychophysical and fMRI experiments. One subject was also an author of the study. All participants provided written informed consent, and the experimental protocol was approved by the Committee for the Protection of Human Subjects at the University of California, Berkeley. Each subject participated in one session to acquire high-resolution whole-brain anatomical MRI images and in one retinotopic mapping fMRI session. Prior to the retinotopic mapping session, each subject practiced the two target detection tasks for a total of four hours in a behavioral testing room, allowing the behavioral performance of the subjects to reach asymptotic levels. In

addition, behavioral data from the practice sessions were used to determine the target sizes for each subject that resulted in equivalent performance of the two tasks in the fMRI experiment.

### fMRI data acquisition

Functional MRI experiments were conducted for five subjects with a 4 Tesla Varian INOVA MR scanner and for three subjects with a 3 Tesla Siemens Trio MR scanner. A transmit/receive surface radiofrequency coil was used to maximize contrast-to-noise ratio in occipital cortex. Functional echo-planar images were acquired using a gradient-echo EPI sequence. The field of view was 180×180 mm (4 T) or 200×200 mm (3 T), and the matrix size was 64×64 (4 T) or 96×96 (3 T), resulting in an inplane voxel resolution of 2.81×2.81 mm (4 T) or 2.08×2.08 mm (3 T). The repetition time (TR) was 1.067 s (4 T) or 2.133 s (3 T), and the echo time (TE) was 28 ms (4 T) or 26 ms (3 T). Twenty (4 T) or twenty-two (3 T) slices were prescribed with an interslice gap of 0.3 mm and a slice thickness of 3 mm (4 T) or 2 mm (3 T). The slices were angled between the coronal and axial planes to provide coverage of occipital and posterior parietal cortex. A set of T1-weighted anatomical images that were coplanar with the EPI images was acquired at the beginning of every imaging session.

### fMRI data preprocessing

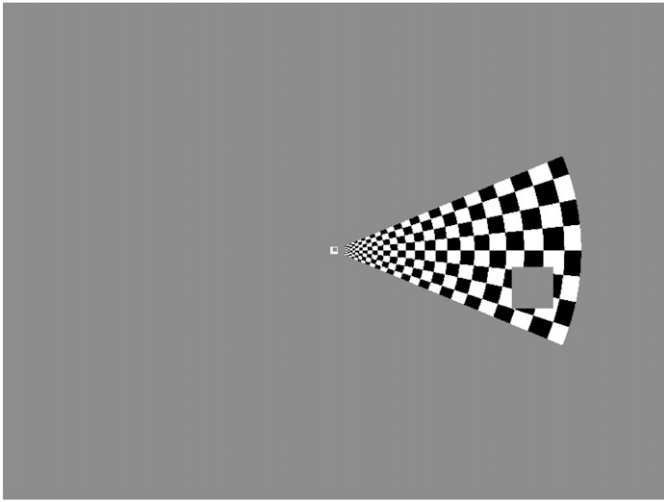
Each run lasted 281.6 s, and the first 8.53 s of the fMRI time series were discarded. Head movements were corrected offline using a 3D image registration algorithm (MCFLIRT; Jenkinson et al., 2002). Finally, each voxel's time series was divided by its mean intensity to convert the data from arbitrary units to percent signal modulation and to compensate for the decrease in mean image intensity as a function of distance from the surface coil. Neither high-pass filtering nor temporal detrending was applied to the time series.

### Visual stimuli

A checkerboard wedge stimulus rotating about a central fixation point (Engel et al., 1994; Engel et al., 1997; Sereno et al., 1995) was continuously presented during acquisition of each fMRI time series. The check size within the stimulus was scaled according to the cortical magnification factor in human V1 (Slotnick et al., 2001), and the stimulus contrast was 100%. Stimuli were presented using MR-compatible goggles (Resonance Technology, Northridge, CA) in the 4 T scanner and an LCD projector (Avotec, Stuart, FL) in the 3 T scanner. The wedge subtended 45 degrees and extended from 0.5 degrees (inner radius) to 10.9 degrees (outer radius) of visual angle (Fig. 1). Each wedge reversed contrast at a rate of 7.5 Hz. The wedge was presented for 2.13 s in each location, and the subsequent wedge location was displaced 22.5 degrees in a clockwise direction. Therefore, there were a total of 16 wedge positions, and each position overlapped 50% with the neighboring positions. The wedge completed a full rotation once every 34.13 seconds. Subjects were instructed to continuously maintain fixation on a central fixation point (0.25 degrees of visual angle) throughout each scan.

### Task

In the attention-to-wedge task, subjects were instructed to maintain fixation on the central point and to press a button whenever they detected a target within the wedge. The target was a square region of zero contrast (luminance equal to mean luminance of the wedge), and the target duration was one full cycle of contrast reversal of the checkerboard wedge stimulus (0.27 s). There was a 50% probability of target presentation at each wedge position, and the target could appear anywhere within the wedge stimulus at unpredictable times. This spatial and temporal uncertainty regarding target presentation



**Fig. 1.** Stimuli and tasks. Subjects maintained fixation while viewing a wedge-shaped stimulus that rotated around the central fixation point. In the attention-to-wedge condition, subjects pressed a button when they detected a contrast decrement target within the wedge. In the attention-to-fixation condition, subjects detected contrast decrement targets within the fixation point. For both attention conditions, contrast decrements were presented in both the wedge and fixation point, but the timing of contrast decrement presentation was independent in the wedge and fixation point.

encouraged subjects to continuously maintain spatial attention over the entire rotating wedge. The target sizes in three eccentricity bands (0.5–4.0, 4.0–7.4, and 7.4–10.9 degrees of visual angle) were scaled to equate the percentage of targets correctly detected for these bands, but the boundaries between the eccentricity bands were not visible to the subjects.

In the attention-to-fixation task, subjects were instructed to maintain fixation on the central point and to press a button when they detected a square region of zero contrast within the fixation point. The targets in the attention-to-fixation and attention-to-wedge tasks had identical durations, contrasts, and probabilities of presentation. During behavioral practice sessions, the size of the fixation target was adjusted to insure that the task difficulty (percentage of fixation targets correctly detected) was equal to that of each of the three eccentricity bands in the attention-to-wedge task.

If necessary, the sizes of the wedge and fixation targets were adjusted during the fMRI experiments to maintain equal performance for each of the three eccentricity bands and for both task conditions for each subject. To equate sensory stimulation in the two tasks, the square zero contrast regions were presented in both the fixation point and the wedge for both attention conditions (although the temporal sequence of presentation within the fixation point and the wedge were independent and were based on a 50% probability of presentation for each wedge position). The attention-to-wedge and attention-to-fixation runs always occurred in pairs, and any changes to the target sizes were applied to both runs in the pair. Thus, the only difference between the two conditions was that the subjects responded to wedge targets in the attention-to-wedge task and responded to fixation targets in the attention-to-fixation task. Eye movements were not recorded during the fMRI experiments. However, all participants were highly trained in maintaining fixation through participation in numerous prior psychophysical experiments.

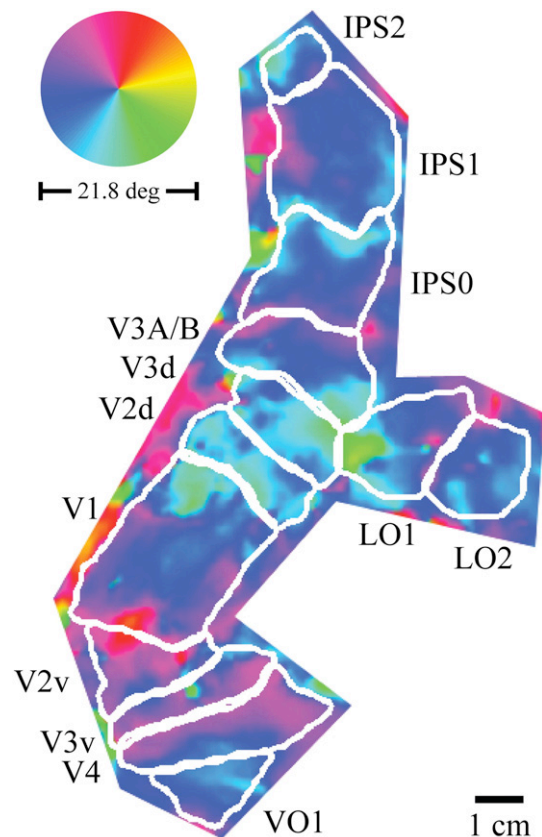
#### Definition of visual areas

The boundaries of visual cortical areas V1, V2, V3, V3A/B, V4, LO1, LO2, and VO1 and posterior parietal areas IPS0, IPS1, and IPS2 were defined using well-established phase-encoded retinotopic mapping methods (DeYoe et al., 1996; Engel et al., 1994; Engel et al., 1997; Sereno et al., 1995; Silver et al., 2005). First, the time series obtained for each voxel were averaged across all runs. In all cases, there were

equal numbers of attention-to-wedge and attention-to-fixation runs. Cortical area boundaries were defined based on this average time series, thereby eliminating potential bias in the definition of areal boundaries in favor of one of the task conditions.

The duration of the stimulus cycle was 34.13 s, resulting in a modulation of fMRI signals in visually-responsive voxels of  $1/34.13 \text{ s} = 0.0293 \text{ Hz}$ . The coherency between a sinusoid of this frequency and the average fMRI time series for each voxel was calculated (Engel et al., 1994; Rosenberg et al., 1989). Computation of coherency generates two quantities: the response phase (the temporal phase of the sinusoid that provides the best fit to the recorded fMRI time series) and the coherency magnitude (the strength of coupling between the best-fit sinusoid and the fMRI time series). The phase corresponds to the delay in the fMRI response relative to the stimulus cycle and is used to estimate the angular component (in polar coordinates) of the visual field location that is represented by a given voxel.

These response phases were spatially transformed into computationally flattened cortical patches (Fig. 2). The visual field maps were of sufficient quality to allow identification of the boundaries of V1, V2, V3, V3A/B, V4, IPS0, IPS1, and IPS2 in both hemispheres of all subjects (total of 16 hemispheres). LO1 was defined in all hemispheres except one (left hemisphere of Subject #2), LO2 was defined in all hemispheres except two (left hemisphere of Subjects #2 and #4), and VO1 was defined in all hemispheres except two (right hemisphere of Subjects #6 and #8). Our slice prescription was chosen to provide coverage of posterior parietal cortex and therefore did not consistently include ventral occipital cortical area VO2.



**Fig. 2.** Visual field representations in occipital and parietal topographic areas. For each voxel, an equal number of attention-to-wedge and attention-to-fixation time series were averaged together, and the response phase (temporal delay of the fMRI response relative to the stimulus cycle) was computed for this average time series. The color wheel indicates the one-to-one mapping between response phase values and the angular component of the visual field location. In this computationally flattened patch of right occipital and parietal cortex (Subject #4), each topographic area represents the contralateral right visual field.

### Time series analysis

Each subject completed between five and seven attention-to-wedge runs and an equal number of attention-to-fixation runs. The order of runs was interleaved for the two attention conditions. For each fMRI run, values of coherency magnitude and phase were generated for each voxel. The coherency magnitude, also known as coherence, is a measure of signal-to-noise ratio of the stimulus response and is equal to the amplitude of the fMRI response at the stimulus frequency divided by the square root of the power across all frequencies in the time series (Engel et al., 1997). Coherence values are bounded by zero and one and are therefore not normally distributed, so they were converted into normally distributed z-scores by Fisher transformation. To quantify the effects of spatial attention on fMRI retinotopic mapping signals, baseline measures of coherence were generated by averaging coherence values from individual attention-to-fixation runs. The percent change in coherence for each attention-to-wedge run relative to this baseline value was then computed to quantify the effects of spatial attention on response reliability.

## Results

### Behavioral results

Subjects viewed a rotating wedge stimulus while maintaining fixation on a central square (Fig. 1). Gray square targets (luminance equal to the mean luminance of the wedge) were presented at random times in both the fixation point and in the wedge, and the timing of target presentation in the fixation point was independent of target presentation in the wedge. On alternating fMRI runs, subjects were instructed to continuously direct their attention to either the fixation point (attention-to-fixation condition) or the wedge (attention-to-wedge condition). They pressed a button every time they detected a target at the attended location. The size of the contrast decrement targets were selected to produce equivalent (approximately 70% correct) behavioral performance for fixation and wedge targets (Table 1) and for targets in each of three eccentricity bands within the wedge (Table 2).

Six of eight subjects showed less than 5% difference in performance on the two attention tasks. However, despite efforts to equate difficulty for both conditions, two subjects performed 10–15% better in the attention-to-wedge condition than in the attention-to-fixation condition (Table 1). However, these differences in performance were not statistically significant for either subject (subject #7:  $p = 0.07$ , two-tailed  $t$ -test,  $n = 6$  pairs of runs; subject #8:  $p = 0.19$ , two-tailed  $t$ -test,  $n = 6$  pairs of runs). We conducted all fMRI analyses after excluding these two subjects and found the same pattern of results that was obtained from the entire group of eight subjects. We therefore report results from all eight subjects. There was no significant group difference in performance for the two attention tasks ( $p = 0.30$ , two-tailed  $t$ -test,  $n = 8$  subjects). The fact that performance on the two tasks was equivalent controls for a number of possible confounds, including differences in fMRI signals due to task difficulty, attentional

**Table 1**

Percentage of targets correctly detected in attention-to-wedge and attention-to-fixation tasks.

Subject	Attention-to-fixation	Attention-to-wedge
1	78	80
2	72	72
3	64	62
4	73	72
5	67	69
6	60	63
7	78	67
8	80	65
Mean	71	69

**Table 2**

Percentage of targets correctly detected in each of three eccentricity bands in attention-to-wedge task.

Subject	Near (0.5–4.0 deg)	Middle (4.0–7.4 deg)	Far (7.4–10.9 deg)
1	74	87	78
2	70	68	81
3	65	68	56
4	74	70	78
5	64	68	72
6	59	55	69
7	67	84	80
8	69	85	87
Mean	68	73	75

effort, and/or arousal. In addition, performance was similar for detecting wedge targets at near, middle, and far eccentricities (Table 2), indicating that the selected relationship between wedge target size and eccentricity encouraged subjects to distribute their attention over the entire stimulus in the attention-to-wedge condition.

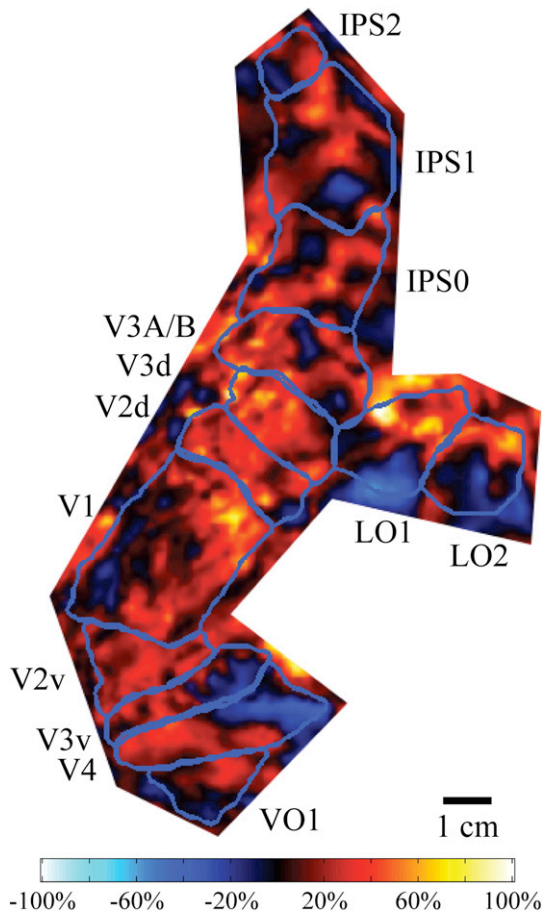
### Attention increases reliability of retinotopic mapping signals

Functional MRI was used to measure the reliability of cortical responses to the rotating wedge stimulus while subjects attended either the wedge stimulus or a central fixation point. The retinotopic mapping stimulus was a high-contrast counterphase-flickering checkerboard wedge that rotated about a central fixation point at a rate of 0.0293 Hz. The coherence between a voxel's fMRI time series and a sinusoid with frequency of 0.0293 Hz is a measure of the signal-to-noise ratio (SNR), or reliability, of the response (Engel et al., 1997). Coherence was computed for every voxel for each run. Because coherence values are bounded by zero and one, they were normalized by transformation into Fisher z-scores. The effect of attending to the rotating wedge was then expressed as the percent change in coherence z-score, relative to the attention-to-fixation baseline condition (Fig. 3 and Supplementary Figs. 1–8). Then, for each run, we averaged these percent change values across all voxels within a topographic cortical area.

Attending to the wedge stimulus substantially increased the reliability of fMRI responses in each defined cortical area ( $p < 0.0001$  in each area, two-tailed  $t$ -test,  $n = 50$  runs). For the group of eight subjects, all areas (V1, V2, V3, V3A/B, V4, IPS0, IPS1, IPS2, LO1, LO2, and VO1) showed increases in reliability that ranged between 20% and 35% (Fig. 4). A similar pattern of results was obtained when assessing reliability for individual subjects (Fig. 5). Area V4 showed significant enhancement of response reliability when attending to the wedge stimulus in all eight subjects ( $p < 0.05$ , two-tailed  $t$ -test,  $n = 5, 6$ , or 7 runs per subject); V1, V2, V3, and VO1 in seven of eight subjects; V3A/B and IPS1 in five subjects; IPS0 and LO1 in four subjects; and IPS2 and LO2 in three subjects. Out of a total of 88 subject and cortical area combinations, only four (Subject #5–LO2 and IPS1; Subject #6–LO1; Subject #8–V3A/B) showed numerical decreases in reliability in the attention-to-wedge condition, and none of these decreases were statistically significant (Fig. 5).

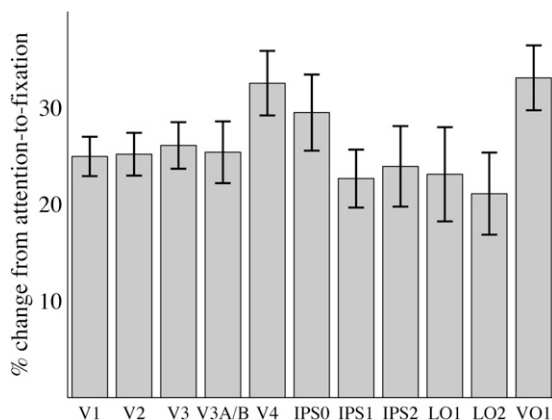
### Attention improves reliability of retinotopic mapping signals for averaged time series

The data presented in Figs. 4 and 5 demonstrate the improvement in SNR for single fMRI runs that results from attending to the wedge stimulus. However, retinotopic mapping analyses are typically performed on time series averaged over several runs. Averaging across runs reduces noise (since the phases of fluctuations at non-stimulus frequencies are generally independent across runs), but preserves signal (since the phase of the evoked fMRI response relative to the visual stimulus cycle is similar across runs). We quantified the increase in response reliability caused by attending to the retinotopic



**Fig. 3.** Attending to the retinotopic mapping stimulus increases reliability of fMRI responses. The average of the z-transformed coherence values for the attention-to-fixation time series served as a baseline for each voxel, and the average percent change in z-score in the attention-to-wedge time series relative to this baseline quantifies the change in response reliability resulting from attending to the retinotopic mapping stimulus. In this example right hemisphere (Subject #4), attending to the wedge increased coherence in all identified topographic areas. Flat maps for all individual subjects are presented in Supplementary Figs 1–8.

mapping stimulus for time series that were averaged across runs. For a given subject, 5–7 attention-to-wedge runs were averaged, and coherence z-scores were computed for the average time series. Anal-



**Fig. 4.** Attending to the retinotopic mapping stimulus increases response reliability. Coherence z-scores were computed for the attention-to-fixation baseline for each topographic area. For each attention-to-wedge run, a coherence z-score was computed for each area, and the effects of attention were expressed as percent change from the attention-to-fixation baseline. Attending to the wedge significantly increased response reliability (coherence) for all eleven areas.

ogous values were computed for the average of an equal number of attention-to-fixation runs for that subject, and the effect of attending to the wedge was quantified as percent change in coherence z-score relative to the mean attention-to-fixation baseline. Compared to analysis of individual runs, attending to the wedge stimulus produced an even greater improvement in SNR when time series were averaged prior to computing reliability (Fig. 6). In early visual areas (V1–V4) and ventral occipital cortex (VO1), attending to the visual stimulus increased reliability by approximately 50%. This effect was more pronounced in higher cortical areas, with reliability increases of approximately 65–90% in IPS0, IPS1, IPS2, LO1, and LO2. In addition, out of a total of 88 subject and cortical area combinations, only one (Subject #6–LO1) showed a numerical decrease (1%) in reliability of the average time series in the attention-to-wedge condition.

*Several attention-to-fixation runs are necessary to achieve reliability that is equivalent to a single attention-to-wedge run*

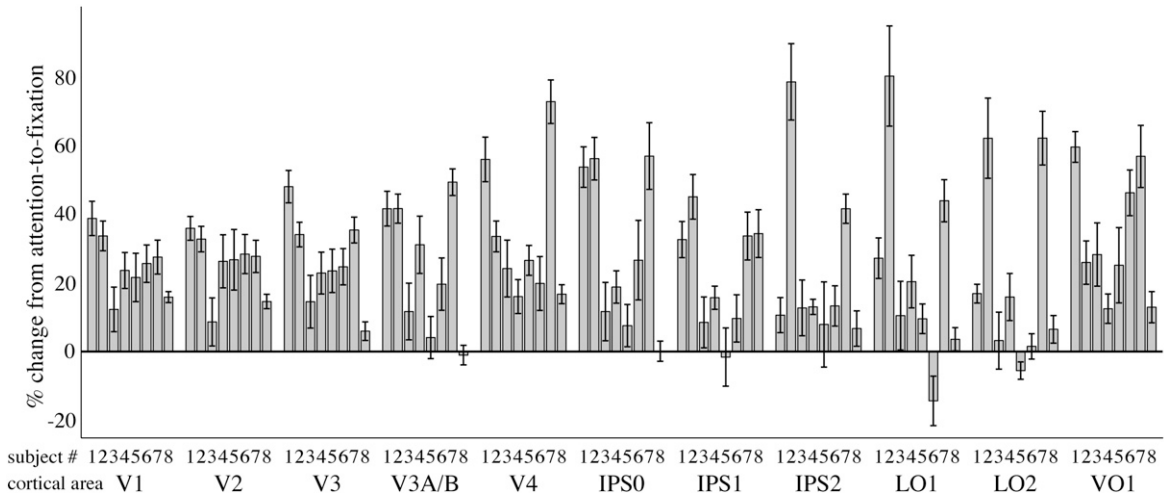
One practical benefit of increased response reliability resulting from attending to the wedge stimulus is that a given SNR value can be reached in fewer fMRI runs. We quantified how many attention-to-fixation runs would be needed to equal the SNR from a single attention-to-wedge run. Coherence z-scores from the first run of the attention-to-wedge condition were compared to z-scores from an average of multiple attention-to-fixation runs. In cortical areas V1–V4 and V3A/B, the reliability of retinotopic mapping responses of a single attention-to-wedge run was equivalent to the reliability of the average of three to five attention-to-fixation runs. That is, for the attention-to-wedge condition, a given SNR was reached in approximately 20–35% of the scan time required to attain the same SNR for the attention-to-fixation condition (Fig. 7). For higher cortical areas (IPS0, IPS1, IPS2, LO1, LO2, and VO1), a single attention-to-wedge run produced greater SNR than the average of five attention-to-fixation runs (Fig. 7).

## Discussion

### *Effects of spatial attention on reliability of retinotopic mapping signals*

Retinotopic mapping has proven to be extremely useful for the objective identification of topographically-organized areas in cerebral cortex (Silver and Kastner, 2009; Wandell et al., 2007). In the present study, subjects either attended to or ignored the rotating wedge stimulus used for retinotopic mapping. We demonstrate that attending to the stimulus increased the SNR of single retinotopic mapping runs by approximately 25% across several occipital and parietal topographic cortical areas. This beneficial effect of attention on response reliability was magnified when comparing averaged time series from the two conditions. In this case, attention increased response reliability by approximately 50% in early visual and ventral occipital areas and 65–90% in higher-order posterior parietal and lateral occipital areas. Our results suggest that retinotopic mapping studies would benefit greatly from requiring subjects to allocate spatial attention to the mapping stimulus.

These findings are highly relevant for researchers seeking to define early visual cortical areas with minimal scanning time: for these areas, the SNR of one run of attention-to-wedge mapping is equivalent to that obtained from an average of 3–5 attention-to-fixation runs. Relative to early visual cortex, posterior parietal and lateral occipital cortical regions showed an even greater improvement in response reliability with attention. In particular, the largest improvement in reliability occurred in posterior parietal (IPS0, IPS1, IPS2) and lateral occipital (LO1, LO2) cortical areas that are often difficult or impossible to define using conventional retinotopic mapping data collection and analysis methods. Our findings in posterior parietal cortex are consistent with previous studies reporting that the relative influence



**Fig. 5.** Attending to the retinotopic mapping stimulus increases response reliability: individual subject data. Conventions are the same as in Fig. 4, but individual data for all eight participants are displayed.

of sensory responses compared to attentional modulation decreases at higher levels of the dorsal visual cortical processing hierarchy (Serences and Yantis, 2006; Silver et al., 2005).

A direct comparison of the effects of averaging and the effects of attending (Fig. 7) provides further evidence that attention signals are particularly important for revealing the organization of higher-order topographic areas: in IPS0, IPS1, IPS2, LO1, LO2, and VO1, even an average of five attention-to-fixation runs did not yield the reliability produced by a single attention-to-wedge run. These results suggest that studies aiming to discover new cortical areas that potentially contain only weak topographic organization would substantially benefit from the inclusion of a task that directs attention to the mapping stimulus. This is supported by the finding that an “attention-to-stimulus” task revealed topographic organization in many higher-order cortical areas but that this organization was not apparent when subjects directed attention to the fixation point (Saygin and Sereno, 2008).

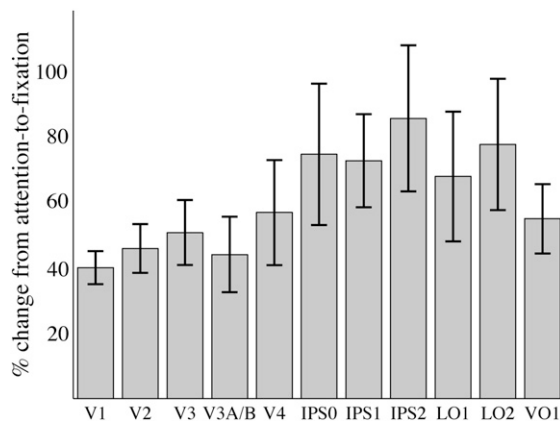
Methodological advances in topographic mapping with fMRI have greatly improved the fidelity of retinotopic maps. Some recent advances include scanning at high magnetic field strength (Hoffmann et al., 2009), employing two simultaneous periodic mapping stimuli (Slotnick and Yantis, 2003), and including an estimate of population receptive field size in the model of the fMRI time course for each voxel (Dumoulin and Wandell, 2008). The spatial and temporal characteristics of the

standard checkerboard wedge stimulus are often chosen based on estimates of receptive field size and temporal frequency tuning of cortical area V1. A number of studies have modified the checkerboard wedge in order to study higher-order areas, including adding color (Swisher et al., 2007), complex spatial patterns (Hansen et al., 2007), biological motion (Saygin and Sereno, 2008), or video of natural images (Sereno and Huang, 2006). Other groups have employed memory-guided saccade, spatial working memory, and/or spatial attention tasks to identify a number of novel topographic areas in parietal and frontal cortex (Hagler and Sereno, 2006; Kastner et al., 2007; Konen and Kastner, 2008; Schluppeck et al., 2005; Sereno et al., 2001; Silver et al., 2005; reviewed in Silver and Kastner, 2009). However, the enhancement of retinotopic mapping responses due to these modifications of the conventional stimuli has not been quantitatively measured. Our results quantify the benefits of attending to the retinotopic mapping stimulus for SNR of single fMRI runs, SNR of averaged time series, and the amount of fMRI scan time required to perform retinotopic mapping.

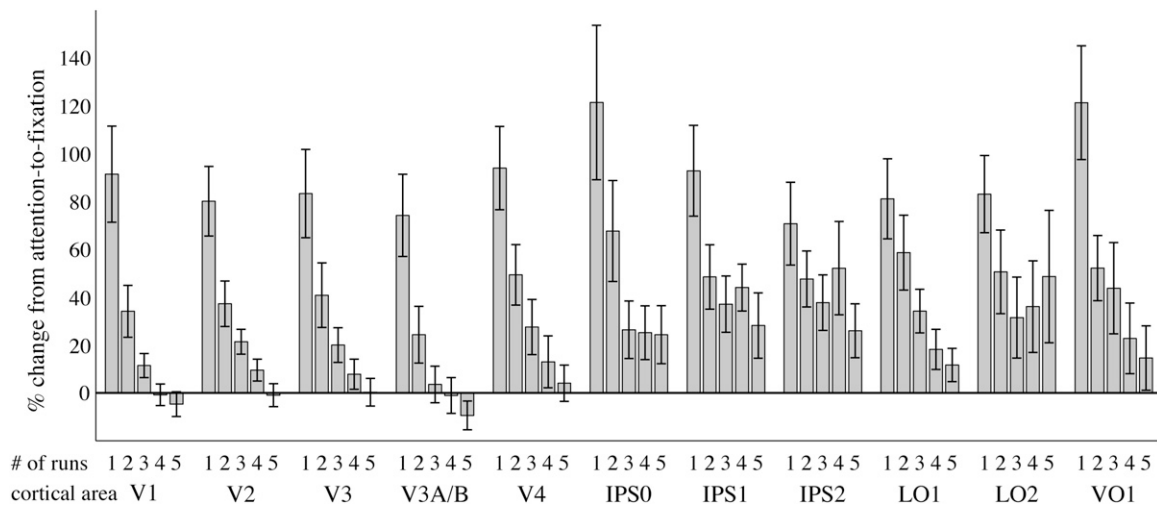
#### *Possible neural mechanisms for the enhancement of response reliability by attention*

The improvement in reliability described in this study indicates that the allocation of attention causes the time course of fMRI responses to more closely match the visual stimulus. This could occur by an increase in the gain of the neuronal response to the visual stimulus. There is substantial evidence that spatial attention enhances neural responses to attended visual stimuli (Bushnell et al., 1981; McAdams and Maunsell, 1999; Motter, 1993; Treue and Maunsell, 1996). In fMRI studies in human early visual cortex, this enhancement by attention is largely independent of stimulus contrast, suggesting that much of it is due to an additive gain increase (Buracas and Boynton, 2007; Li et al., 2008; Murray, 2008). Indeed, allocation of spatial attention selectively increases fMRI responses in portions of early visual cortex that represent attended locations, even in the absence of visual stimulation (Kastner et al., 1999; Silver et al., 2007).

Recent evidence suggests that the spatially-specific effects of attention on fMRI responses in early visual areas may be modulated by top-down attention signals from IPS1 and IPS2. These posterior parietal cortical areas contain a topographic map of the contralateral visual field but respond poorly to visual stimuli that are not attended (Silver et al., 2005). A direct link between attention signals in IPS1/2 and those in visual cortex comes from fMRI functional connectivity measurements during sustained spatial attention in the absence of visual stimulation. Relative to fixation, sustained spatial attention increases the strength of coupling between IPS1/2 and several visual



**Fig. 6.** Attending to the retinotopic mapping stimulus increases response reliability in averaged fMRI time series. Conventions are the same as in Fig. 4, except that the time series within a given attention condition were averaged before computing coherence. Attending to the wedge significantly increased response reliability (coherence) for all eleven areas.



**Fig. 7.** Comparison of the effects of attending to the retinotopic mapping stimulus versus averaging multiple attention-to-fixation runs. The coherence for the first attention-to-wedge run was computed and compared to the coherence of an average of one to five attention-to-fixation runs. For early visual cortical areas, three to five attention-to-fixation runs must be averaged in order to obtain a coherence value that is comparable to a single attention-to-wedge run. For posterior parietal, lateral occipital, and ventral occipital cortical areas, an average time series of five attention-to-fixation runs exhibits lower response reliability than a single attention-to-wedge run.

cortical areas (Lauritzen et al., 2009). Additionally, analysis of the temporal relationships among these areas during sustained attention indicates that IPS1/2 leads several early visual cortical areas by a few hundred milliseconds (Lauritzen et al., 2009). Therefore, it is likely that IPS1 and IPS2 transmit spatially-specific top-down attention signals to early visual cortex.

In addition to an additive gain increase, an alternative (but not mutually exclusive) mechanism for attention to improve SNR is a reduction in brain activity that is unrelated to the visual stimulus. Independent of the effects of attention on the amplitude of visual responses, a reduction in spontaneous fluctuations of fMRI signals would improve SNR. There is recent evidence that attention improves reliability of representations of visual stimuli in monkey V4 neurons by decreasing interneuronal correlations in firing rate that are unrelated to the stimulus (Cohen and Maunsell, 2009; Mitchell et al., 2009). Additional studies are needed to clarify the mechanisms by which attention improves the reliability of fMRI signals in topographic cortical areas.

It is unlikely that artifacts due to eye movements contributed significantly to our results. Although we did not record eye movements, all participants were highly trained at maintaining fixation in visual psychophysical experiments. Even if there were significant eye movements away from fixation in the attention-to-wedge condition, this would change the mapping between visual field location and retinal location, thereby reducing reliability of fMRI responses to the wedge stimulus. However, we found a robust increase in response reliability in the attention-to-wedge condition in all subjects and all identified cortical areas, suggesting that the benefits of spatial attention outweigh any potential artifacts due to eye movements.

#### *Contributions of spatial attention in previous studies of topographic organization of parietal and frontal cortex*

Other fMRI topographic mapping studies have used tasks that, although not explicitly manipulating attention, may have involved spatial attention. Hagler and Sereno (2006) employed a spatial working memory task to reveal topographic maps in frontal and prefrontal cortex, and a memory-guided saccade task has been used to map topographic areas in parietal cortex (Schluppeck et al., 2005; Sereno et al., 2001), parietal and superior frontal cortex (Hagler et al., 2007), and frontal cortex (Kastner et al., 2007). Both of these tasks require visual spatial attention, and the results of these studies are consistent

with the attentional enhancement of fMRI retinotopic mapping signals we have found. However, the experimental design we have used has substantial advantages for characterizing the effects of attention on the representation of visual stimuli in a large number of cortical areas. Unlike the memory-guided saccade task, eye position is stable throughout the recording in our covert attention task. In addition, comparison of attention-to-wedge and attention-to-fixation conditions allows quantitative assessment of the effects of attending to the stimulus without stimulus or task difficulty confounds.

Swisher et al. (2007) reported robust topographic mapping signals in IPS1 and IPS2 despite the fact that subjects continuously maintained their attention at the fixation point. The same task was used to discover two novel topographic areas in parietal cortex, IPS3 and IPS4. These results appear to be at odds with the current study, in which we emphasize the importance of attending to the periodic mapping stimulus, especially for posterior parietal cortical areas. It is notable that Swisher et al. (2007) employed a novel mapping stimulus that contained bright flashing colors embedded in the rotating checkerboard wedge. Since behavioral performance on the central fixation task in the Swisher et al. (2007) study was greater than 95%, it is possible that the dynamic color changes in the rotating wedge drew attention to the retinotopic mapping stimulus. This could explain the difference between the findings of Swisher et al. (2007) and those of previous studies using monochromatic periodic mapping stimuli that failed to detect topographic organization in posterior parietal cortex. While Swisher et al. and others have argued for using a central attention task to improve fixation stability during fMRI retinotopic mapping, our direct comparisons of attention-to-fixation and attention-to-wedge conditions suggest that the benefits of covertly attending to the retinotopic mapping stimulus outweigh possible improvements in fixation stability resulting from attending to the fixation point. An important topic for future research is the characterization of the relative contributions of exogenous and endogenous attention to response reliability in the brain.

#### **Conclusions**

Recent methodological advances have greatly improved the fidelity of fMRI retinotopic mapping, enabling precise descriptions of the representation of the visual field in early visual cortical areas as well as the discovery of new topographically-organized regions. In this study, we quantified the benefits of attending to a retinotopic mapping stimulus

and found that attention improves the reliability of averaged fMRI responses in early visual and ventral occipital cortex by approximately 50%. This enhancement in response reliability was even greater in posterior parietal and lateral occipital cortical areas. Our results are of particular importance for the study and discovery of regions with topographic organization of signals that are not purely sensory. In addition, employing an attention task greatly increases the efficiency of retinotopic mapping: it requires no extra scanning time, and a single attention-to-wedge run generates retinotopic mapping signals with a reliability equivalent to that of an average of several attention-to-fixation runs for the same visual stimulus. Finally, attention increased the SNR of retinotopic mapping responses in every cortical area that was studied and at multiple levels of the visual processing hierarchy, thereby demonstrating the generality of the beneficial effects of spatial attention on the reliability of neural representations of sensory stimuli.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2010.06.063](https://doi.org/10.1016/j.neuroimage.2010.06.063).

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