Effects of Attention on Physiological Responses in Human Visual Cortex

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Abstract

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Behavioral performance often suffers when attention is divided across multiple visual items. These results are supported by fMRI experiments showing reduced responses during divided attention, relative to focused attention, in primary visual cortex. However, a subset of behavioral research on divided attention suggests that the costs of dividing attention are dependent on task complexity and stimulus type. For example, costs are typically minimal when searching for a constant target that is defined by simple features such as orientation or contrast. Here we show fMRI evidence in humans that shows no cost of dividing attention in a task that incorporates simple search, on responses in primary visual cortex. Observers determined whether or not a vertically oriented low-contrast Gabor patch was present within one or four relevant locations. All four locations were always occupied by horizontally oriented Gabor pedestals, and the probability of a target being present was independent across trials and locations. Only the number of relevant locations varied across conditions. We found that the BOLD signal measured from human V1 was not reduced by divided attention when the task and stimuli are simple, suggesting that neural processing of simple features in primary visual cortex has unlimited capacity, corroborating a recent finding in monkeys (Chen and Seidemann, 2012).

Multiple visual tasks can be performed on the same visual input, with different tasks presumably engaging different neuronal populations. The modular layout of the visual system implies that specific cortical regions carry more information about certain stimulus attributes than others.

Thus, it is reasonable to assume that decisions during a task will be optimal if they are based on the responses of the most informative neuronal signals, which presumably originate in regions with the sharpest tuning for the relevant stimulus feature. Previous studies have supported this position. Here we present the results of two fMRI experiments that confirm these findings and expand on earlier investigations by addressing the effects of the physical properties of an attended stimulus on task-related modulations in human visual cortex. Specifically, we ask whether performing two-alternative forced choice speed- and color-discrimination tasks (and other attentional processes) can modulate neural activity independent of visual stimulation, and whether the effect of spatial attention depends on which task is being performed. The results indicate that, (1) when stimulation and spatial attention are constant, responses in V4 and MT+ depend on the task being performed, and are independent of the tested physical properties of the selected stimulus, (2) this task-dependent modulation might require a stimulus – task-specific preparatory mechanisms alone are not sufficient to drive responses, and (3) independent of which task is being performed, spatial attention adds a baseline shift to responses in MT+ and V4 when a stimulus is present.

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effective teaching. Over the past couple of years, I have been lucky to work closely with John Palmer on the project which makes up Chapter 1 of this dissertation. His scientific thoroughness is exemplary, and his knowledge of behavioral psychology seemingly encyclopedic.

When I first started working for Scott in the summer of 2007, what would eventually become the *Vision and Cognition Group* was in its infancy. Since then, I am honored to be associated with, and to be acquainted with, the many individuals who have been a part of the combined labs. They have all left their separate marks on me, and I will never forget any of them. Memories of conferences, lab outings, late nights, and problems solved, are the signatures of an era for me.

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A General Introduction

At any given time we can only be aware of a small subset of the total information available to our sensory systems. The phenomena of selectively enhancing important and relevant information and suppressing less relevant information are often considered collectively under the header of "attention." How does the human nervous system accomplish selection and suppression, and where are these processes instantiated? This dissertation is concerned with specific questions related to the effects of attentional states on neural processing of visual information. The first set of questions address neural capacity limits during divided spatial attention to multiple sources, and the second set of questions address the effects of the task used to maintain attention.

I used functional magnetic resonance imaging (fMRI) as my primary investigative tool. FMRI provides an indirect measure of neural activity known as the blood-oxygen-level-dependent (BOLD) signal, which has been shown to be proportionate to local neural activity over a small window of both space and time (Heeger and Ress, 2002). Although much remains uncertain about the causal relationship between BOLD and neural responses, it is currently the best available proxy for the neural activity underlying cortical processing of human psychological phenomena.

The first chapter of the dissertation deals with the effects of selective and divided attention on the BOLD signal in primary visual cortex. Selective attention refers to situations where only a single source of information is relevant to an observer's current task or behavioral goal, such as when trying to listen to a conversational partner at a loud party. In the domain of vision, information presented in an attended spatial location is reported more quickly and with higher accuracy than information presented elsewhere (e.g. Posner, 1980; Kahneman and Treisman, 1984; Shulman et al., 1985; Palmer and Moore, 2009). In contrast, divided attention requires monitoring of multiple sources of information, such as when driving. Experimentally, behavioral performance during divided attention often fails to achieve the same level as during selective attention to a single source (Eriksen and Spencer, 1969; Shiffrin and Gardner, 1972; Anderson et al., 1998). In general, the more spatial locations that become relevant, the smaller the performance advantage over irrelevant locations.

Since the advent of fMRI, many studies have revealed that selective spatial attention produces an increased BOLD signal in areas of cortex representing an attended location relative to unattended locations (e.g. Tootell et al., 1998; Brefcynski and DeYoe, 1999; Gandhi et al., 1999; Murray, 2008). Comparatively few fMRI studies have investigated the effect of divided attention on physiological responses. Using various experimental paradigms and analysis techniques, the studies that have been published suggest reduced neural responses when attention is distributed across multiple stimuli relative to when focused on a single stimulus (Müller et al., 2003; McMains and Somers, 2005; Pestili et al., 2011; Anderson et al., 2013).

However, a recent optical imaging study found no difference in V1 signal change between focal and distributed attention conditions (Chen and Seidemann, 2012). Importantly, a few design factors differentiated their experimental paradigm from those of the fMRI studies, including task and stimulus complexity. Chapter 1 documents a study attempting to repeat the key manipulations of Chen and Seidemann (2012) using fMRI. I wanted to evaluate whether the influence of these factors affect the previously established finding of reduced BOLD responses in primary visual cortex during divided attention.

Chapter 2 explores the relationships between attentional selection, the type of task used to maintain selection, and spatial attention, on BOLD responses in different areas of human visual cortex. I was particularly interested in areas MT+ and V4. These two areas have been implicated in the processing of motion and color, respectively. In a hypothetical fMRI experiment, suppose one periodically alternated between presenting a moving achromatic stimulus (ex: a field of moving gray dots) and a stationary chromatic stimulus (ex: a field of stationary colored dots). Ideally, we would expect the resulting BOLD signal measured from MT+ to be fit quite well by a sine wave (shifted by an estimate of hemodynamic delay); similarly, the signal from V4 would be well fit by the same sine wave shifted by half a period.

If we altered the experiment by spatially superimposing our two stimuli as two transparent surfaces and presenting them simultaneously, instructing our subjects to periodically select (attend to) first the moving surface, and then the colored surface, what might we predict the BOLD signal to look like? Given that the ‘preferred’ stimulus attributes by which MT+ and V4 are modulated by are both continuously present, we might not expect any periodicity within the signal from either area. However, previous research predicts that our surface-based selection manipulation could in fact modulate the signal (at least within MT+; O’Craven et al., 1997; Valdes-Sosa et al., 2000, 2001).

Now, imagine a single stimulus composed of both motion and color. What happens to the signal measured from these areas? Since there is no change in the stimulus attributes by which MT+ and V4 are strongly modulated, we might expect no significant signal change. However, this is not always the case. Previous work has suggested that even when the same stimulus is being selected, performing tasks requiring the analysis of motion and color modulates MT+ and V4, respectively (e.g. Corbetta et al., 1990, 1991; Beauchamp et al., 1997; Chawla et al., 1999;

Huk and Heeger, 2000). Thus, the relevant information guiding attentional selection is an important factor. If we asked subjects to periodically attend to first the motion, then the color (i.e. by performing a discrimination task), we might expect the same periodicity in our signal as in the initial situation.

The two modifications outlined above demonstrate instances where attention can modulate physiological responses in a situation where stimulation is constant; the only thing that changed were the instructions to the subjects – change which surface you attend to, change the task you are performing. The study described in Chapter 2 looks at the relationships between surface selection and task type, and how their effects might interact in shaping physiological responses within early visual cortex. Additionally, we analyzed whether or not the effect of spatial attention was independent of task.

Dividing attention across simple features: Evidence for unlimited capacity processing in primary visual cortex

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In collaboration with:

John Palmer, Scott O. Murray, Zachary R. Ernst, & Geoffrey M. Boynton

Behavioral performance often suffers when attention is divided across multiple visual items. These results are supported by fMRI experiments showing reduced responses during divided attention, relative to focused attention, in primary visual cortex. However, a subset of behavioral research on divided attention suggests that the costs of dividing attention are dependent on task complexity and stimulus type. For example, costs are typically minimal when searching for a constant target that is defined by simple features such as orientation or contrast. Here we show fMRI evidence in humans that shows no cost of dividing attention in a task that incorporates simple search, on responses in primary visual cortex. Observers determined whether or not a vertically oriented low-contrast Gabor patch was present within one or four relevant locations. All four locations were always occupied by horizontally oriented Gabor pedestals, and the probability of a target being present was independent across trials and locations. Only the number of relevant locations varied across conditions. We found that the BOLD signal measured from human V1 was not reduced by divided attention when the task and stimuli are simple, suggesting that neural processing of simple features in primary visual cortex has unlimited capacity, corroborating a recent finding in monkeys (Chen and Seidemann, 2012).

INTRODUCTION

Visual selective attention has been researched extensively, especially for spatial attention. Behavioral results demonstrate that observers detect and discriminate information presented within an attended spatial location more quickly and accurately than information presented elsewhere (e.g. Posner, 1980; Kahneman and Treisman, 1984; Shulman et al., 1985; Palmer and Moore, 2009; Yiğit-Elliott et al., 2011). Physiologically, spatial selective attention increases the spiking rate of neurons, as well as fMRI responses, in areas of cortex selective for the attended location (e.g. Desimone and Duncan, 1995; Treue and Maunsell, 1996; Tootell et al., 1998; Brefcynski and DeYoe, 1999; Gandhi et al., 1999; Murray, 2008). Evidence suggests that physiological effects of attention are causally linked to behavioral benefits (Ress et al., 2000).

Divided attention often leads to decreased behavioral accuracy and increased response times compared to selective attention (e.g. Kahneman, 1973; Anderson et al., 1998; Harris et al., 2004). In the visual domain, such costs are especially evident for relatively complex tasks, such as word and object-discrimination (e.g. Shaw, 1984; Harris et al., 2004; Scharff et al., 2011). Unlike for selective attention, less is known about the neural correlates of divided attention. The few fMRI studies on divided attention have found V1 blood-oxygen-level-dependent (BOLD) signal reductions during divided attention relative to selective attention (Müller et al., 2003; McMains and Somers, 2005). Two recent studies applying quantitatively advanced analyses found similar effects in V1, characterized by decreased selection efficiency (Pestili et al., 2011) and reduced precision of stimulus representations (Anderson et al., 2013) during divided attention. These studies suggest that neural responses are in some way reduced when attention is distributed across multiple stimuli, perhaps providing the physiological basis for reduced behavioral performance under such conditions.

Unlike previous studies showing deficits for divided attention, a recent optical imaging study (Chen and Seidemann, 2012) found a striking lack of signal difference in monkey V1 between selective and divided attention conditions.

One potential reason for the discrepancy between Chen and Seidemann (2012) and other studies (Müller et al., 2003; McMains and Somers, 2005; Pestili et al., 2011; Anderson et al., 2013) is that behavioral capacity limitations during divided attention may depend on the complexity of the task and relevant stimuli (Shaw, 1984; Palmer, 1994; Busey and Palmer, 2008; Scharff et al., 2011). Findings of behavioral divided attention effects using complex stimuli and/or tasks are in line with the physiological effects found by Müller et al. (2003) and McMains and Somers (2005) which used feature conjunctions and letters, as well as with Anderson et al. (2013), which implemented a change detection task, and Pestili et al. (2011), where elements of change detection appeared in a complex task. In contrast, Chen and Seidemann (2012) trained monkeys to perform a simple visual search for the presence of horizontal Gabor patches among vertical patches. Such stimuli match the spatial response profiles of many V1 neurons well (Movshon et al., 1978; Heeger, 1992).

Here we used fMRI to study neuronal responses in V1 when attention is divided across multiple sources during a simple visual search task and found, like Chen and Seidemann (2012), no reduction in V1 responses when attention was divided relative to when attention was directed to only a single source. We also found no behavioral deficit for dividing attention. This supports the hypothesis that for certain simple tasks, divided attention can come at no cost compared to selective attention.

METHODS

Subjects

6 subjects (3 males, 3 females) participated in the study, ranging in age from 23 to 31. One of the subjects was author ER. All subjects gave written and informed consent in accord with the human subjects Institutional Review Board at the University of Washington, had normal or corrected-to-normal vision, and were compensated $20/hr.

Stimulus & procedure

Throughout each phase of the experiment, the following procedure was applied during single trials (see Figure 1 for a schematic). The subject began each trial by foveating a square on the center of a gray screen (gray: 50% of max luminance). At the start of each trial, a short oriented black line appeared close to fixation for 500 ms, pointing to the location(s) to be attended on that trial (four possible locations: one in each quadrant of the visual field).

After a variable stimulus-onset interval (SOI, varied between 0 and 1700 ms), four horizontally oriented circular Gabor patches (2 cycles per degree, Gaussian standard deviation of 1 deg, 20% contrast) appeared simultaneously within each quadrant (one per quadrant, centered 5.66 degrees diagonally from fixation). Each of these patches acted as a pedestal for a potential target stimulus: a vertically oriented Gabor patch of varying contrast (typically between 1.0 – 1.7%; during fMRI experiment: constant within subjects and across conditions). The appearance of a target was randomly generated with a probability of .275, independently across trials and locations. This value was chosen so that the probability of a target appearing during the focal conditions was the same as a target *not* appearing during the distributed condition $(1-.275)^4$. Pedestals and targets appeared simultaneously, remained on the screen for 300 ms, and then disappeared simultaneously.

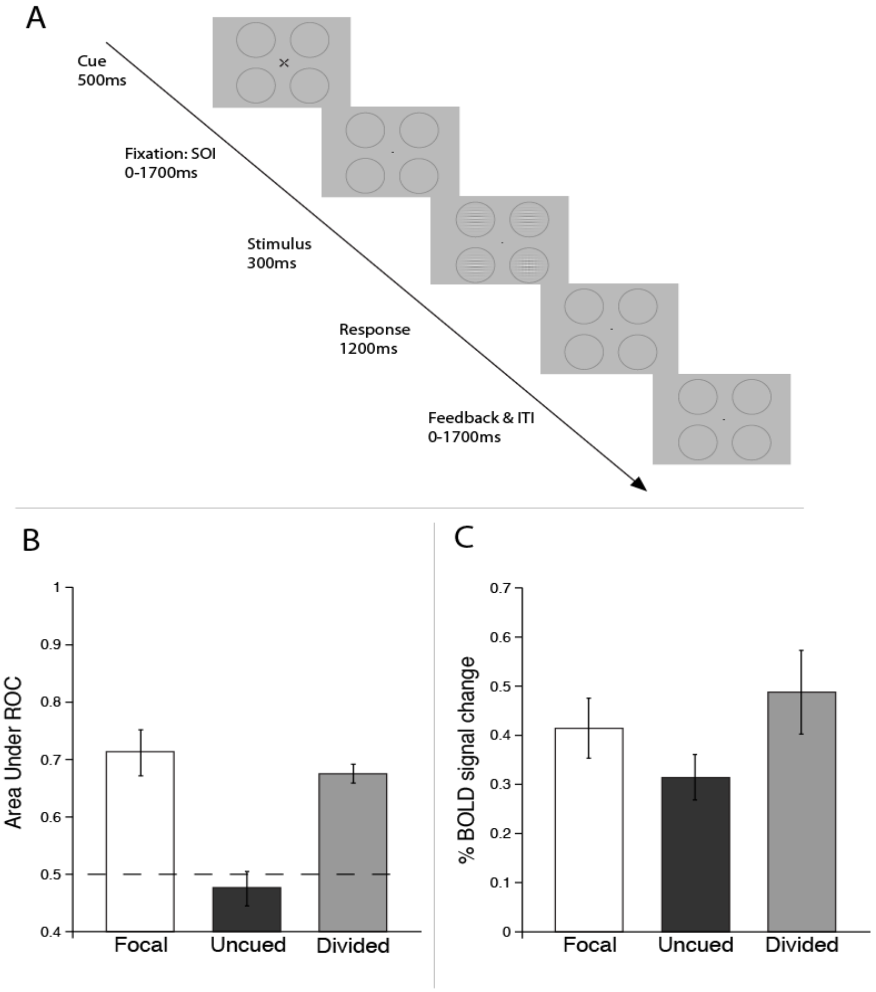

Figure 1. A) Procedure during a single trial. Cue could be directed to one of the four visual quadrants (focal), or all four quadrants (distributed). Size of cue exaggerated for purpose of demonstration. B) Mean behavioral performance during fMRI experiment across subjects. A_g: area under ROC curve (see text for computational details); error bars represent 1 SEM across subjects. Dashed line represents chance performance. C) Mean percent BOLD signal change across subjects; error bars represent 1 SEM across subjects.

The subject's task was to report their perceptual confidence that a target had appeared in the attended location(s), on a scale from 1 to 4, where 1 = "very unlikely," 2 = "unlikely," 3 = "likely," and 4 = "very likely." The window for submitting a response ended 1500 ms after stimulus onset. Immediately after response submission or response window expiration, feedback was provided by changing the color of the fixation square to either green (correct), red (incorrect), or yellow (no response); the "likely" and "unlikely" confidence ratings were collapsed for the purposes of feedback. After a variable interval, the next trial was initiated by the appearance of the attention-directing cue(s).

Design

The key experimental manipulation involved the number of attended sources. Subjects attempted to detect low-contrast oriented Gabor targets superimposed on orthogonal pedestals, while attending to either one or four locations. Each subject participated in a single fMRI scanning session, preceded by practice sessions carried out both in the laboratory as well as in the scanner. These sessions are described in detail below.

fMRI session: We collected 16 scans in total from each subject: two spot localizer scans, two standard retinotopic mapping scans, and 12 experimental scans.

During the experimental scans, subjects performed trials of the target-detection task. Across trials within a scan, subjects were always cued to direct their attention to the same location(s). Attentional state was manipulated between scans: selective attention was directed to one of the four visual field quadrants during two scans each ("focal" conditions), and attention was divided across the four quadrants during the remaining four scans ("distributed" condition).

Each experimental scan began with a 12-second fixation interval, and was followed by interleaved 16-second trial intervals and fixation intervals (6 of each). The trial intervals contained four 4-second trials. At the beginning of each trial interval, low-contrast circular outlines appeared around the four stimulus locations (co-centered with stimuli, radius 3 deg) and remained on the screen for the duration of the interval. Responses were collected using a magnet-compatible fiber-optic key-press device.

Importantly, there were no stimulus-related differences between scans and between conditions (excepting the attention-directing cue); the probability of a target appearing in any of the four locations was always constant and independent across locations, trials, and conditions. The only manipulation was in terms of attentional selection.

Practice sessions: Subjects spent several hours practicing the different conditions in the laboratory in front of a CRT monitor prior to scanning, to familiarize themselves with the stimuli, task, and response mapping. A secondary purpose was to choose appropriate target contrast levels for each subject so that performance would be well away from floor and ceiling in both focal and distributed conditions. Stimulus properties such as size, pedestal contrast, and background contrast were matched to those used in the subsequent scanning sessions, and subjects used a keyboard to make their responses. For practice only, we reduced the duration of the fixation intervals in the interest of saving time, from 12 seconds to 3.

A second practice session took place with subjects performing the task while lying in the bore of the scanner (no fMRI data collected) in order to assimilate the subject with the exact conditions to be encountered during the imaging experiment. Also, due to differences in display equipment, the appropriate target contrast levels estimated in the lab often needed to be slightly adjusted for the scanner environment. Around one hour per subject was devoted to practice in the scanner.

Display equipment

During practice in the laboratory, the stimuli were generated and displayed via a Dell Inspiron 530 desktop computer and presented on a 41 cm ViewSonic 690fB CRT monitor. During sessions conducted in the scanner, the stimuli were generated using a Dell Studio 1558 laptop and back-projected onto a fiberglass screen via an Epson Powerlite 7250 projector. Stimuli for all experiments were created with Matlab software (MathWorks) and presented using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

fMRI data acquisition

FMRI data were acquired in a Phillips 3T scanner at the Diagnostic Imaging Science Center at the University of Washington. Functional images were acquired using an echo planar sequence, with a 32-channel high-resolution head coil. We used a repetition time of 1 s and echo time of 30 ms. Eighteen axial slices (80 × 80 matrix, 220-mm field-of-view, no gap) were collected per volume (voxel size: 2.75 x 2.75 x 3.4 mm). Anatomical images were acquired using a standard T1-weighted gradient echo pulse sequence. All preprocessing (anatomical-functional coregistration, conversion to standardized Talairach space, slice-scan time correction, motion correction, and linear trend removal) was performed using BrainVoyager™. Subsequent analyses were carried out using custom software written in Matlab.

Defining regions of interest

We used standard phase encoding retinotopic mapping procedures to define visual areas V1, V2, V3, and V4 (Engel et al., 1994). We then restricted the regions of interest (ROIs) to the area of visual space stimulated during the experimental scans using the spot localizer data. Using this procedure, we successfully delineated the retinotopic locations of all four stimuli in V1, but were unable to find reliable activation in all four quadrants within V2 – V4, presumably because of the relatively small Gaussian envelope used in the spot localizer (standard dev. = 1 deg). We therefore restrict our analyses to V1.

fMRI data analysis

Preprocessed experimental time-courses were imported into Matlab for analysis. For each individual voxel included in the analysis of a given ROI (V1 contained four ROIs: one corresponding to each visual field quadrant), percent signal change was computed for each individual trial interval by normalizing by the mean response over the last three timepoints of the preceding fixation interval. Normalized timepoints 7-16 were then averaged across voxels, trial intervals, and scans of identical conditions to produce five summary data points per ROI – one for each of the four selective attention conditions, and one for the divided attention condition. We used these to calculate the effects of selective attention and divided attention on fMRI responses.

In order to calculate the effect of selective attention, we first averaged the four focal condition summary data points across ROIs to generate the "focal mean." For each focal condition, we then collected the summary data points from the ROI representing the visual quadrant diagonally opposite to the attended location. These four summary points (across focal conditions) were averaged together to generate the "uncued mean." The uncued mean was subtracted from the focal mean on a within-subject basis, and the effect of selective attention was derived by taking the mean of the differences.

Similarly, the effect of divided attention was calculated by first computing the distributed mean by averaging the distributed condition summary data points across all four ROIs. The distributed mean (the distributed condition summary data point) was then subtracted from the focal mean on a within-subject basis, and the mean of the differences computed.

Behavioral data analysis

We collected behavioral responses during the imaging experiment, and assessed them using a signal detection analysis (Green and Swets, 1966), using our four response categories as representing different response boundaries between target present/absent, thereby generating four points on an ROC (Reciever Operating Characteristic) curve. The area under the curve (A_g) was used to characterize behavioral performance.

We conditionalized the ROC analysis to include only trials that contained only one or zero targets, because performance with multiple targets would likely be biased due to the "redundant target effect" (Shaw, 1984) whereby irrelevant targets increase the probability of hits and false alarms. Each point on the focal and distributed ROC curves represented the probability of a hit (responding to a target and the cued location(s)) and the probability of a false alarm (responding to a target at the uncued location(s)), at the four criterion response levels. At the lowest criterion, all trials for which at least a response of "very unlikely" was given are included (all trials), yielding hit and false alarm probabilities of 1.0. At the highest criterion, only the trials for which at least a response of "very likely" was given are included, yielding low hit and false alarm probabilities.

Each point on the uncued ROC represents the probability of an "uncued hit" (the probability of responding "target present" when there is no target at the attended location, but one target at one of the uncued locations), and the probability of an "uncued false alarm" (the probability of responding "target present" when there is no target at the attended location, and no targets at any of the uncued locations).

		Focal		Uncued	Distributed	
Subject	Target contrast	% correct	A_g	A_g	% correct	A_g
S1	1.5%	77.1	0.85	0.55	76.0	0.71
S2	1.7%	81.8	0.75	0.38	60.0	0.62
S3	1.3%	67.7	0.53	0.53	54.2	0.48
S4	1.4%	64.6	0.60	0.43	64.6	0.69
S5	1.4%	72.9	0.64	0.45	72.9	0.71
S6	1.5%	69.8	0.72	0.55	71.9	0.65

Table 1. Behavioral performance during fMRI experiment. Percent correct includes all trials. A_g calculation conditionalized on number of targets presented during trial (see text).

Green's area (Pollack and Hsieh, 1969), or $A_{g,}$ the area under the ROC curve, was computed by sequentially connecting each of the four points with a straight line that began at the origin, and calculating the geometric area contained below that line. One subject (S3) produced A_g values very near 0.5 (chance detection) during all conditions. Thus, there was no evidence to suggest that S3 was attending and responding as directed, and this subject was removed from all other analyses. Single-subject behavioral data is shown in Table 1.

To assess the effect of selective attention on target detection, we computed the mean difference in A_g between the focal and uncued conditions within subjects. Similarly, the effect of divided attention was derived by computing the mean difference in A_g between the focal and distributed conditions.

RESULTS

Behavioral performance

Selective attention: The effect of selective attention on target detection was assessed by comparing the A_g values from the focal and uncued conditions within subjects. The difference, 0.24, was significant (SEM = 0.04, dependent-samples $t = 6.01$, $p < 0.01$), indicating that subjects were more likely to detect and respond to targets appearing within the cued location than within the uncued locations.

Divided attention: A primary aim of the study was to confirm previous findings suggesting that there is no effect of divided attention when the relevant information is composed of simple features (Palmer, 1994; Chen and Seidemann, 2012). The mean difference in A_g between the focal and distributed conditions, 0.04, was not significant (SEM = 0.05, dependent-samples $t = 0.73$, $p > 0.1$); within our experimental paradigm, there was no behavioral cost to dividing attention across multiple sources relative to attending to a single source. The mean A_g across subjects for all three primary conditions is plotted in figure 1b.

fMRI responses

Selective attention: Within observers, the effect of selective attention was significant, with a mean difference in BOLD signal change of 0.1% between the focal mean and uncued mean (SEM = 0.04%, dependent-samples $t = 2.62$, $p < .05$). This was the case regardless of which, or how many, of the irrelevant ROIs were included in the calculation of the uncued mean.

Divided attention: The primary goal of the experiment was to characterize the effect of dividing attention across multiple sources of information on responses in primary visual cortex, relative to when only a single source is relevant. The effect of divided attention was slightly negative (-0.07%) and not significant (SEM = 0.07%, dependent-samples $t = -1.07$, $p > .1$). Figure 1c displays the mean percent signal change from baseline across subjects for all three summary conditions.

Modeling an effect of divided attention

The statistical comparisons of the focal and distributed conditions suggest null effects of dividing attention across multiple sources on both fMRI and behavioral responses, relative to selective attention to a single source. However, it is important to consider the cases that would in fact allow us to reject the null hypothesis of no effect. It is reasonable to assume that A_g values from the distributed condition should not exceed those from the focal condition, and that they should not fall below those from the uncued condition. If dividing attention within the current experimental paradigm does incur a behavioral cost, distributed A_g values should fall somewhere between the upper and lower bounds established by the focal and uncued conditions. The question is, were our measured responses during the distributed condition significantly different from what would be predicted based on a model that assumed that attention could not be efficiently distributed to all locations during a given trial?

We adopted an all-or-none mixture model to simulate a hypothetical case where attention could be devoted to only a single location during any given trial of the divided attention condition. Under such a model, attention randomly selects one of the four locations for full processing on a single trial. The probability of a single location being attended on a given trial is then 0.25. Averaging across all locations and trials, this model leads to a predicted behavioral sensitivity (A_g) during the distributed condition that is one quarter of the way between the measured uncued A_g and the focal A_g. Within subjects, the mean difference between the predicted distributed A_g and the measured distributed A_g was significant (mean difference = 0.14, SEM = 0.03, dependent-samples $t = 4.25$, $p < .05$). Assuming this all-or-none mixture model is a fair approximation of strong capacity limitations, we can tentatively accept the notion that subjects efficiently selected more than a single location on any given trial during the distributed condition.

The same model was applied to the imaging data. We again assumed that attention could only select one of the four locations for full processing on a given trial, which leads to a predicted percent BOLD signal change during the distributed condition that is equal to one quarter of the way between the measured uncued and focal percent BOLD signal changes. Within subjects, the mean difference between the predicted distributed BOLD signal change and the measured distributed BOLD signal change, 0.15%, was not significant (SEM = 0.08%, dependent-samples $t = 1.78$, $p > .1$).

DISCUSSION

The primary goal of this experiment was to test the hypothesis that divided attention, when implemented via visual search for simple features, does not reduce physiological responses in human V1, relative to selective attention. Previous fMRI research has shown robust effects of divided attention, but these studies utilized relatively complex classes of stimuli and/or complex change detection tasks. Our stimuli and task are similar to a recent optical imaging study in monkeys (Chen and Seidemann, 2012) in which the presence/absence of oriented Gabor patches were detected in precued locations.

We replicated the findings of many previous studies showing effects of selective attention on both behavioral and physiological measures. We used A_g, the area under the ROC curve, as our measure of behavioral sensitivity. Sensitivity to stimuli presented within the spatial locus of selective attention (cued location) was higher than to stimuli presented outside of it (uncued locations). Similarly, fMRI responses within areas of V1 selective for particular spatial locations were higher when attention was allocated to those locations than when it was allocated elsewhere.

Historically, states of divided attention have been strongly associated with decreases in behavioral performance (e.g. Kahneman, 1973; Anderson et al., 1998; Harris et al., 2004), revealing capacity limitations. However, a collection of previous work has shown that processing of multiple sources is unlimited in capacity when the attention-guiding task and relevant information are fairly simple (e.g. Palmer, 1994; Huang and Pashler, 2005; Patterson, 2006; Busey and Palmer, 2008; Scharff et al., 2011). Consistent with these studies, we found that dividing attention across locations containing oriented Gabor patches had no effect on behavioral sensitivity (A_g), relative to selective attention to a single stimulus location. Our study implemented a very similar experimental paradigm as that of Chen & Seidemann (2012), who found no effect of divided attention on macaque V1 optical imaging responses. Similarly, we found that divided attention did not reduce human V1 BOLD responses relative to when attention was focused on a single stimulus location.

The present study highlights what is essentially the finding of a null result: neither behavioral sensitivity nor the BOLD signal originating from primary visual cortex were affected by divided attention (relative to selective attention). In this case (and in such cases generally), it can be informative to model a specific instance where dividing attention across two or more sources without a loss of sensitivity is not possible, and predict the effect on behavior and BOLD signal. A comparison between the predictions of such a model and our measurements can yield some insight into the possible cases that would in fact allow us to reject the null hypothesis of no effect. To this end, we implemented a simple all-or-none mixture model to simulate a hypothetical case where attention could be devoted to only a single location during any given trial of the divided attention condition. The outcome of this modeling exercise led us to tentatively accept the notion that subjects could efficiently select more than a single location during the distributed condition without a loss of behavioral sensitivity, but not necessarily that our measured BOLD signal could be reliably differentiated from the BOLD signal predicted by a strict limitation on the distribution of neural resources across multiple sources.

There is disparity between our physiological results and those of earlier studies. In the introduction, we mentioned four investigations which all showed effects of divided attention on responses in primary visual cortex (Müller et al., 2003; McMains and Somers, 2005; Pestili et al., 2011; Anderson et al., 2013). The two earlier studies utilized stimuli which can qualitatively be labeled complex (color and shape conjunctions; letters) relative to the tuning properties of neurons within V1, compared to the oriented Gabor patches used in the current experiment.

Behavioral evidence suggests that detection of color and shape conjunctions is often a serial process, and thus subject to capacity limitations (e.g. Treisman and Gelade, 1980). Although there are lots of examples of unlimited capacity processing of letters (e.g. Eriksen and Spencer, 1969; Pashler and Badgio, 1987), when targets and distractors are both letters, as in McMains and Somers (2005), evidence suggests that detection is indeed subject to capacity limits (Schneider and Shiffrin, 1977; Kleiss and Lane, 1986). We propose that the differences in stimulus class between our experiment and those of Müller et al. (2003) and McMains and Somers (2005) might at least partially account for the different physiological results.

Anderson et al. (2013) implemented change detection as their means of controlling attention whereas we used visual search. The key difference between these tasks is how target stimuli are defined and presented. In a search task, the target stimulus never changes (in our experiment, it was always a vertical Gabor patch of constant contrast); in a change detection task, the identity of a target stimulus depends on the state of the 'comparison' or 'standard' stimulus. For example, Anderson et al. (2013) asked observers to detect and discriminate threshold orientation changes (clockwise or counter-clockwise) of one or two attended gratings. The orientation of the standard grating(s) changed from trial to trial, which implies that the orientation of the possible targets also changed from trial to trial, and was thus dependent on the state of the standard. Similarly, Pestili et al. (2011) presented gratings within each visual quadrant, each with a different contrast on a trial-to-trial basis. Observers were instructed to detect whether or not an increment in contrast (a target) occurred between two stimulus intervals within one or all of the quadrants (pre-cue vs. post-cue conditions). In this case, the rule for detecting a target was also stimulus-specific.

Change detection tasks tend to produce large set-size effects on behavioral performance (Scott-Brown and Orbach, 1998), relative to visual search. The main hypotheses for why this phenomenon occurs involve limits on memory and/or decision. First, it is necessary to encode and retain a memory of an initial display in order to detect a change in a subsequent display. Additionally, a memory of a first display must not only be maintained and retrieved, but also compared to a second display (decision). Both encoding processes (e.g. Irwin, 1992; Rensink, 2002) and decision processes (Scott-Brown et al., 2000; Hollingworth, 2003) have been found to affect change detection. Obviously, these processes are not mutually exclusive. We propose that the involvement of memory processes required by change detection tasks contributed to the divided attention effects on V1 fMRI responses in Anderson et al. (2013), and potentially in Pestili et al. (2011).

While Pestili et al. (2011) and Anderson et al. (2013) both found physiological differences between selective and divided attention conditions, the two investigations attributed them to different processes. Pestili et al. (2011) concluded that the best explanation for their results was enhanced selection efficiency of the relevant stimulus during focal-cue trials (selective attention) relative to distributed-cue trials (divided attention). In contrast, Anderson et al. (2013) found that voxel population response profiles became less selective for their preferred orientations during divided attention relative to selective attention, leading them to conclude that the precision of perceptual representations of relevant stimuli become degraded when attention is divided. The contrast between these conclusions highlight a long-standing debate within behavioral attention research: does attention affect the stimulus representation directly, or does it affect decision processes? According to signal detection theory (e.g. Green and Swets, 1966; Tanner, 1956, 1961), the internal representations of percepts are inherently noisy. Even if single sources are processed completely independently of other sources, the theory predicts small effects of divided attention simply because each additional source increases the chance of false alarms. Several experiments have found support for the “decision hypothesis” using simple visual search tasks (e.g. Palmer et al., 1993; Palmer, 1994; Scharff et al., 2011), and imply that there is no need to invoke any direct effect of attention on physiological stimulus representations per se during simple task conditions, which is in line with the results of the current study.

The present results suggest that the unlimited capacity results of similar behavioral experiments (e.g. Palmer, 1994; Scharff et al., 2011) might be physiologically based on the independent availability of neural resources across regions of primary visual cortex tuned to different areas of visual space. Such independence is plausibly restricted to relatively simple stimuli like oriented Gabors and gratings, which characterize the spatial response properties of V1 neurons very well (Movshon et al., 1978; Heeger, 1992). V1 neurons and their responses may provide the underlying substrate required for performing such detection tasks. Previous work has shown that fMRI responses in visual areas demonstrating preference for specific stimulus features (such as MT+ and motion) increase when tasks are performed requiring the analysis of those features (speed or direction discrimination), implicating those areas as providing possible neural bases for the performance of different visual tasks (Corbetta et al., 1990, 1991; Beauchamp et al., 1997; Runeson et al., 2013).

Conclusions:

We have found evidence that fMRI responses in V1 are not affected by dividing attention across stimuli defined by simple features relative to when selecting a single such stimulus, using a visual search task. This is in contrast to previous fMRI studies showing strong signal reductions during divided attention. We propose that the lack of an effect in the current study reflects independent processing across space by discrete sets of neurons within primary visual cortex tuned to the features defining our stimuli. The use of a simple visual search task avoided any involvement of memory processes, which are implicated in large behavioral set size effects. Our findings corroborate those of Chen and Seidemann (2012), showing evidence of unlimited capacity processing of simple features in primary visual cortex.

Effects of Task and Attentional Selection on Responses in Human Visual Cortex

In collaboration with:
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Multiple visual tasks can be performed on the same visual input, with different tasks presumably engaging different neuronal populations. The modular layout of the visual system implies that specific cortical regions carry more information about certain stimulus attributes than others. Thus, it is reasonable to assume that decisions during a task will be optimal if they are based on the responses of the most informative neuronal signals, which presumably originate in regions with the sharpest tuning for the relevant stimulus feature. Previous studies have supported this position. Here we present the results of two fMRI experiments that confirm these findings and expand on earlier investigations by addressing the effects of the physical properties of an attended stimulus on task-related modulations in human visual cortex. Specifically, we ask whether performing two-alternative forced choice speed- and color-discrimination tasks (and other attentional processes) can modulate neural activity independent of visual stimulation, and whether the effect of spatial attention depends on which task is being performed. The results indicate that, (1) when stimulation and spatial attention are constant, responses in V4 and MT+ depend on the task being performed, and are independent of the tested physical properties of the selected stimulus, (2) this task-dependent modulation might require a stimulus – task-specific preparatory mechanisms alone are not sufficient to drive responses, and (3) independent of which task is being performed, spatial attention adds a baseline shift to responses in MT+ and V4 when a stimulus is present.

INTRODUCTION

Multiple visual tasks can be performed on the same visual input. When viewing an object, such as a tree, one can analyze its shape for its utility to climb, its color to assess the season, its motion to estimate wind speed, or the shadow it casts to determine the position of the sun. While the visual input remains the same, the different tasks presumably engage different populations of neurons in different computational strategies. How attention can engage these populations to achieve optimal task performance has been a long standing question in visual neuroscience.

One principle of visual system organization which may aid in this process is the largely modular layout of visual cortex (Zeki and Bartels 1998). While the degree of functional modularity is open to debate, it is well-known that different regions of visual cortex contain neurons that are tuned to different visual features. For example, color and motion are processed in two interacting but largely separate streams of processing (Vaina 1994; Van Essen and Gallant 1994; Gegenfurtner and Hawken 1996). In particular, there is evidence that neuronal responses in V4 and MT+ underlie at least some of the perceptual attributes of color and motion, respectively (Salzman et al. 1990; Zeki and Bartels 1999; Conway et al. 2007; Brouwer and Heeger 2009). As a result of a modular organization, a specific neuronal population will carry more information about a particular stimulus component, such as direction of motion, than will others. Consequently, during a specific visual task, such as speed- or color-discrimination, it is reasonable to assume that decisions will be optimal if they are based on the responses of the most informative neuronal signals, which presumably originate in the populations with the sharpest tuning for the relevant stimulus feature(s).

Two decades ago, Corbetta et al. (1990, 1991) performed the first investigations into the effects of selectively attending to different stimulus attributes on responses in human visual cortex. Estimating neuronal responses with Positron Emission Tomography (PET), they reported different foci of activation during tasks involving discrimination of speed, color, and shape of an otherwise physically unchanging stimulus. Subsequent functional magnetic resonance imaging (fMRI) experiments expanded upon these findings. For example, Beauchamp et al. (1997) demonstrated that responses in MT+ increase when observers discriminate the speed of a moving field of dots compared to when discriminating color. Similarly, Chawla et al. (1999) found that when observers were cued to detect a motion or color change in an otherwise stationary monochromatic dot field, responses in MT+ and V4 increased, respectively, even if no change occurred. Huk and Heeger (2000) compared responses in V1, V3A, and MT+ during speed and contrast discrimination of both moving dots and moving gratings. Regardless of the stimulus, responses in MT+ were higher during speed compared to contrast discrimination. Together, these studies suggest that the behavioral goal of the observer increases the gain in neuronal populations tuned to task-relevant information, perhaps increasing the signal-to-noise of informative neurons in order to optimize task performance. Note that these findings stand in contrast to results suggesting that attention to any feature of an object facilitates the neuronal representation of all features of that object (Desimone and Duncan 1995; Valdes-Sosa et al. 1998; O’Craven et al. 1999).

In addition to these task-related modulations, previous studies have shown that selecting a surface or object results in area-specific modulations. For example, O’Craven et al. (1997) demonstrated that when covert attention is directed to a moving random dot field, fMRI responses in MT+ increase relative to when attention is directed to a spatially superimposed static random dot field. Such surface-specific effects of selective attention have also been found in single neurons in area MT of the macaque (Wannig et al. 2007). These results suggest that if an attended object or surface contains the physical properties for which a particular population of neurons is selective for, the response of those neurons increases.

Just as the visual cortex is organized in a modular fashion for specific stimulus attributes, the retinotopic organization of the early visual areas means that these areas are in a sense modularly organized for spatial position. Similarly, just as performing a task modulates fMRI signals in areas associated with the attended stimulus attributes, spatial attention modulates responses within retinotopic maps associated with the attended position (Gandhi et al., 1999; Martinez et al., 1999; Somers et al., 1999). These spatial attention effects appear to be largely independent of the properties of the physical stimulus, and have been typically modeled using a baseline shift in response magnitude (Murray 2008; Buracas and Boynton 2007; however, see Li et al. [2008] for evidence that inclusion of contrast-gain mechanisms account for a larger proportion of spatial attention effects than a baseline shift alone). Thus, it appears that performing a task on a stimulus at a specific spatial location modulates cortical regions associated with both the task and spatial location. What is not firmly established is the relation between task-specific and spatial attention mechanisms; specifically, whether or not they are independent.

Here we present the results of two fMRI experiments that independently varied the task, spatial attention, and properties of the attended stimulus, in order to reveal the individual contributions of these factors to the population responses of different visual areas. We focus exclusively on two-interval forced-choice speed- and color-discrimination tasks. In Experiment 1 we address how the effects of performing these tasks are related to the physical properties of the attended item. For example, does performing a color task on a moving stimulus result in task-related modulations (e.g., in V4), stimulus-related modulations (e.g., in MT+), or some combination of the two? In Experiment 1, we manipulated task type and selective attention to one of two superimposed dot surfaces. The results strongly suggest that task – and not the physical properties of a selected stimulus – is the primary contributor to attention-driven modulations in V4 and MT+. In Experiment 2 we ask whether task and spatial attention can modulate neural activity independent of visual stimulation, and whether the effect of spatial attention depends on task. We manipulated these three factors independently in an event-related design; on a given trial, observers could perform either task on a stimulus of variable dot density, and attend to the left or the right visual field. Overall, the results of Experiment 2 suggest that a stimulus is required for task-specific modulation, the effects of spatial attention do not depend on stimulus strength (as long as a stimulus is present), and that response modulation by spatial attention is independent of what task is being performed. Overall, the results show that the effects of task, stimulus strength and spatial attention each have independent effects on fMRI responses within a given visual area. This lack of dependence gives us confidence that results from previous studies that manipulated only one of these factors (task, stimulus strength or spatial attention) generalize to changes in the other factors.

EXPERIMENT 1:

METHODS

Subjects

Eight subjects participated (four males), ranging in age from 23 to 41. One of the observers was author ER. All subjects gave written and informed consent in accord with the human subjects Institutional Review Board at the University of Washington, had normal or corrected-to-normal vision, and were compensated $20/hr. Each observer took part in the following: two one-hour sessions in the lab for practicing the experimental conditions, two one-hour psychophysics sessions in the scanner, and two scanning sessions. One of the scanning sessions consisted only of retinotopic mapping scans, and the other consisted of experimental scans and localizer scans. One observer was unable to complete the study, and data from another were unusable due to excessive head motion and excluded from analyses.

Stimuli

Two overlapping surfaces of limited-lifetime dots were presented peripherally within a circular aperture (centered at four degrees above and seven degrees to the left or right of fixation) on a black background. The diameter of the aperture was six degrees, and the overall dot density within the aperture was 2.65 dots/deg^2. The fields were distinguished by their direction of motion, such that one field was moving upwards at an average of 2.0 deg/sec, and the other remained nearly static (a small amount of threshold horizontal motion energy was sometimes added to permit speed discrimination task – see below). The fields also differed in color, such that if one field was red, the other was green (figure 2A). Stimuli for all experiments were created with Matlab software (MathWorks) and presented using the Psychophysics Toolbox (Brainard 1997; Pelli 1997).

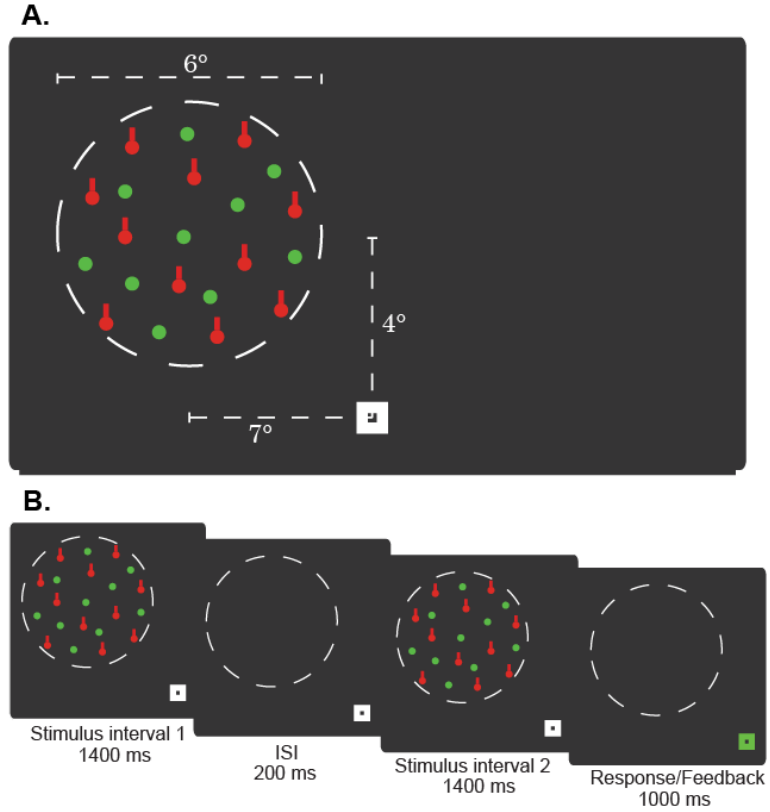

Figure 2. A) Schematic of stimulus used during all phases of Experiment 1 (laboratory practice, scanner psychophysics, fMRI scans). Colors of the dots composing moving and static surfaces were counterbalanced across blocks/scans (one was always green, the other red). In this example, vertical lines attached to the red dots indicate coherent upward movement. Dashed gray circles depict the extent of stimulus apertures (not present during the experiment). B) Procedure for a given trial – Exp. 1. Example: observer attends to the speed of the red surface, and responds with the interval during which the speed of that field was greatest. Color change during response/feedback interval indicated whether or not response was correct (green: correct, red: incorrect). Trial structure was identical for all phases of the experiment.

Display apparatus

During practice in the laboratory, the stimuli were generated and displayed via a Dell Inspiron 530 desktop computer and presented on a 41 cm ViewSonic 690fB CRT monitor. During threshold measurements in the scanner and during fMRI data acquisition, the stimuli were generated using a Dell Latitude D610 laptop and back-projected onto a fiberglass screen via an Epson Powerlite 7250 projector.

Procedures

Practice: Figure 2B outlines the procedure for a given trial. During lab practice, observers performed blocks of two-alternative forced-choice (2AFC) discrimination trials on either the speed or color of the moving or static surface. As either surface could be red or green, and the stimuli could be presented in either the left or right visual field, a total of 16 condition blocks were necessary to include all possible combinations of attended stimulus and task (2 surfaces x 2 tasks x 2 color combinations x 2 locations). Practice was distributed over two days.

Within a single practice block, consisting of 64 trials, the attended surface, color combinations, and the task being performed remained constant. A trial began with a brief fixation period, followed by two 1400 ms stimulus intervals separated by a 300 ms inter-stimulus interval. Between the intervals, the color and speed of both surfaces independently varied; if observers performed the wrong task or attended to the wrong stimulus, performance would be at chance (50%). Following the second interval, observers responded by pressing the key corresponding either to the interval that contained the fastest moving dots (if discriminating speed), or the interval when the color of the dots was chromatically more red or chromatically more green (if discriminating color). In order to permit speed discrimination of the static surface, a small amount of horizontal motion energy (a few pixels per interval) was added during one of the intervals. Color was varied for each surface by adding or subtracting RGB increments within a predetermined range, so that the perceived chromaticity of the surfaces never overlapped, but remained within the perceptual domains of green and red, respectively. The magnitude of the change in the task-relevant feature of the attended surface was determined by a three-down one-up staircase, and was closely matched by the change magnitudes in the unattended features. Responses were collected using the number pad on a standard keyboard. Immediately afterwards, accuracy feedback was provided by changing the color of the fixation mark (green = correct, red = wrong).

Psychophysical threshold measurements: In an effort to equate difficulty across conditions, we estimated psychophysical thresholds for each subject and condition. Psychophysical thresholds were measured in the scanner prior to the fMRI experiment. While lying in the bore of the scanner, observers performed the exact same experimental blocks that were performed in the lab. Responses were collected using a magnet-compatible fiber-optic key-press device.

After the scanner psychophysics sessions were completed, Weibull functions were fit to the data using a maximum likelihood procedure to estimate the speed or color increment that would produce 79% correct performance during each condition. These thresholds were then implemented in the experimental fMRI session; implemented thresholds were averaged across visual fields, but not across the color of the attended surface, which could be either red or green.

fMRI: experimental session: Four main conditions were included. These were products of two independent variables (attended surface, task) with two levels each. Observers attended to either the moving or static field of dots, and performed either a speed discrimination or color discrimination task by attending to the appropriate feature of the stimulus.

The experimental session consisted of eight experimental and two localizer scans. Each experimental scan lasted 5 minutes, 36 seconds and consisted of twelve 20-second condition blocks preceded by 8-second fixation intervals. During the last 3 seconds of each fixation interval, the condition of the upcoming block was cued by changing the color of the fixation mark (green: attend to greenish surface, color task; red: attend to reddish surface, color task; yellow border: attend moving surface, speed task; yellow fill: attend static surface, speed task). Each block was made up of five trials of the cued condition. Each trial proceeded exactly as described above, but the increment change of each feature (attended and unattended) between intervals was constant across trials and determined by the estimated thresholds. Each condition was repeated three times during each scan, and 24 times in total (12 repetitions per hemifield). Stimuli were always presented in one side of the visual field within each scan, and in alternating sides between scans. The order of conditions within and across scans was arranged so that each condition succeeded the other conditions as equal a number of times as possible.

Defining regions of interest (ROI)

The fMRI experimental sessions also included a localizer scan that was repeated twice. These scans were designed to localize both MT+ and regions of cortex that responded preferentially to chromatic over isoluminant gray stimuli. The scan alternated between 20 seconds of a blank screen, 20 seconds of coherently moving dots, 20 seconds of static dots, and 20 seconds of static chromatic dots. The stimulus was always isoluminant, and restricted to the areas of visual space stimulated in the experimental scans.

Visual area MT+ was defined as the voxels showing a greater response to moving than to isoluminant static dots at a Bonferroni-corrected threshold. Only those voxels exceeding the threshold and located near the typical anatomical location of MT+ (posterior to the intersection of the lateral occipital sulcus and the inferior temporal sulcus [Watson et al. 1993]) were considered.

Color-selective regions were defined as the voxels responding more to chromatic than to isoluminant gray dots at a Bonferroni-corrected threshold. Using this contrast, the most significant voxels were consistently located on the ventral surface of the occipital cortex, and corresponded to a subregion of V4, which was defined in a separate retinotopy session (see below). This localizer could only reliably define color-selective regions in four out of the six observers (possibly due to factors related to vascular interference in this region of cortex – see Winawer et al. 2010).

On a separate day prior to the experimental scanning session, we defined visual areas V1, V2, V3, V4, and V3A using standard retinotopic mapping procedures. Once defined, we restricted the ROIs within each of these regions to the area of visual space stimulated during the experimental scans. In light of recent experimental evidence, we assumed a full hemifield representation in V4 (Winawer et al. 2010).

fMRI data acquisition

FMRI data were acquired in a Phillips 3T scanner at the Diagnostic Imaging Science Center at the University of Washington. Functional images were acquired using an echo planar sequence, with an 8-channel head coil. We used a repetition time of 2 s and echo time of 30 ms. Thirty-two axial slices (64 × 64 matrix, 220-mm field-of-view, 0.5mm gap) were collected per volume (voxel size: 3.5 x 3.4 x 3.4 mm). Anatomical images were acquired using a standard T1-weighted gradient echo pulse sequence. All preprocessing (anatomical-functional coregistration, conversion to standardized Talairach space, slice-scan time correction, motion correction, and linear trend removal) was performed using BrainVoyager. Subsequent analyses were carried out using custom Matlab code.

fMRI data analysis

Preprocessed experimental timecourses were imported into Matlab for analysis. In Experiment 1, individual voxel timecourses within ROIs were averaged together to produce a mean timecourse for each ROI per scan. These timecourses were segmented into their constituent blocks and normalized to percent signal change from the average of the last two timepoints of the preceding fixation period. Normalized timepoints 4-10 were then averaged together for each block and across blocks of the same condition to produce one summary data point per ROI per condition.

Eye tracking

During the experimental scanning sessions, eye position was monitored using an ASL LRO6 eye tracking system to ensure that observers maintained fixation for the duration of the scan. Eyenal (version 2.93) was used to convert the data into a text file. Custom Matlab code was then used to analyze the data to determine if the extent of gaze deviation was significantly different between the experimental conditions. Fixation position was monitored during the experimental scans to ensure that any potential differences in signal change between conditions could not be accounted for by differences in eye movements. Due to problems with lens refraction, these measurements were noisy in three out of the six observers, and could not be analyzed reliably. The data from the remaining three observers were analyzed in two different ways. First, the proportion of total frames during which eye position deviated by a criterion distance of one degree from the center of the fixation mark was computed for each observer. This proportion did not differ between the four main conditions for any of the three data sets that were analyzed. Second, we compared mean horizontal eye position for when the stimulus was presented on the right versus when it was presented on the left. Fixation position did not vary as a function of which hemifield was stimulated, and thus attended, in any of the three observers. We also looked for, and failed to find, a difference in mean horizontal eye position between the two stimulation intervals.

RESULTS

Behavioral performance: We monitored behavioral performance during the imaging experiment. Overall, observers' performance across conditions matched well with their estimated thresholds. Average percent correct was 81.96 and 79.70 when the moving surface was attended and speed and color discrimination tasks were performed, respectively. When the static surface was attended, average percent correct was 80.83 and 77.25 for speed and color discrimination tasks. Performance did not significantly vary as a function of task-surface combination (one-way ANOVA, *p* = 0.34), nor as a function of surface color (one-way ANOVA, p = .65). Performance data for individual observers are presented in Table 2.

	Moving Surface		Static Surface	
Subject	Speed	Color	Speed	Color
S1	78.4% (25.1)	82.4% (22.5)	79.2% (0.21)	66.1% (20.0)
S2	82.4% (18.7)	71.2% (12.5)	81.0% (0.17)	73.5% (14.0)
S3	78.3% (9.1)	81.7% (9.5)	77.5% (0.07)	79.7% (9.5)
S4	81.5% (18.6)	82.4% (14.5)	89.2% (0.18)	79.0% (16.0)
S5	89.7% (19.4)	87.5% (20.0)	73.1% (0.17)	87.5% (19.0)
S6	81.4% (10.5)	73.1% (11.5)	85.0% (0.10)	77.8% (15.0)

Table 2. Experiment 1: Task performance during fMRI. Values are percent correct on each of the four main conditions, averaged across hemifields. "Moving Surface" columns: performance when the moving surface was attended; "Static Surface" columns: performance when the static surface was attended; "Speed" columns: performance during speed discrimination conditions; "Color" columns: performance during color discrimination conditions. Discrimination thresholds are provided within parentheses (speed discrimination: deg/sec; color discrimination: RGB increments)

fMRI responses: fMRI data were collected while observers performed speed and color discrimination tasks at threshold difficulty. Eight scans were collected for each observer; during four of these, the stimuli were always presented in the left visual field, and during the other four, in the right visual field. Results did not differ as a function of visual field or color of the attended surface, so data were collapsed across hemispheres and surface color. Figure 3 shows percent signal change for all conditions in all ROIs, averaged across subjects. Error bars indicate one standard error.

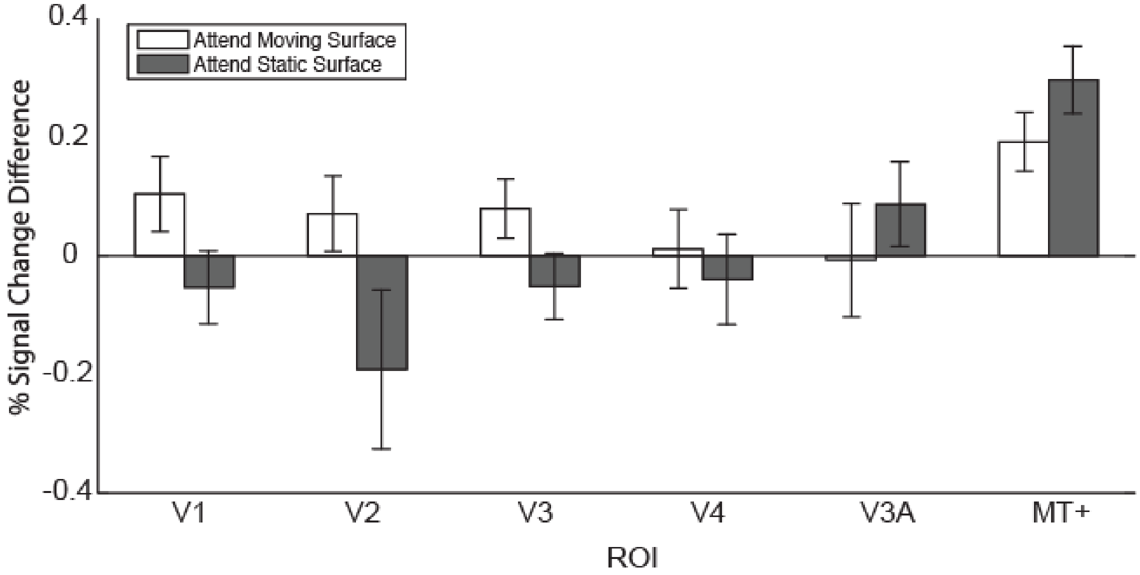

Figure 3. Experiment 1. FMRI responses in areas V1, V2, V3, V4, V3A, and MT+, averaged across six observers. All data are from the stimulated hemisphere. Bar heights represent percent signal change from the preceding fixation block. The effect of task was only significant in MT+, and there were no significant effects of attended surface in any visual area. Error bars represent one standard error of the mean.

To test for any effects of attended surface and task, we conducted a two-way repeated measures (2WRM) ANOVA on the percent signal change in each ROI (V1, V2, V3, V4, V3A, and MT+). A significant effect of task was found in MT+ ($p < .0005$, $n = 6$), but not in any of the other ROIs. Percent signal change from baseline was significantly higher in MT+ during speed discrimination blocks than during color discrimination blocks. Surprisingly, we found no modulation by attended surface in MT+ (contrary to previous findings [O'Craven et al. 1997]), nor in any other ROI. Percent signal change in MT+ was similar during the 'attend moving' and the 'attend static' conditions, in terms of both magnitude and difference between the task conditions (figure 4a); the difference in MT+ response between speed-task and color-task conditions was slightly larger when attention was directed to the static surface (not significant), which might be due to noise or a small task-difference between conditions. The task during the speed-task/attend-moving condition is essentially a motion-detection task (during which interval

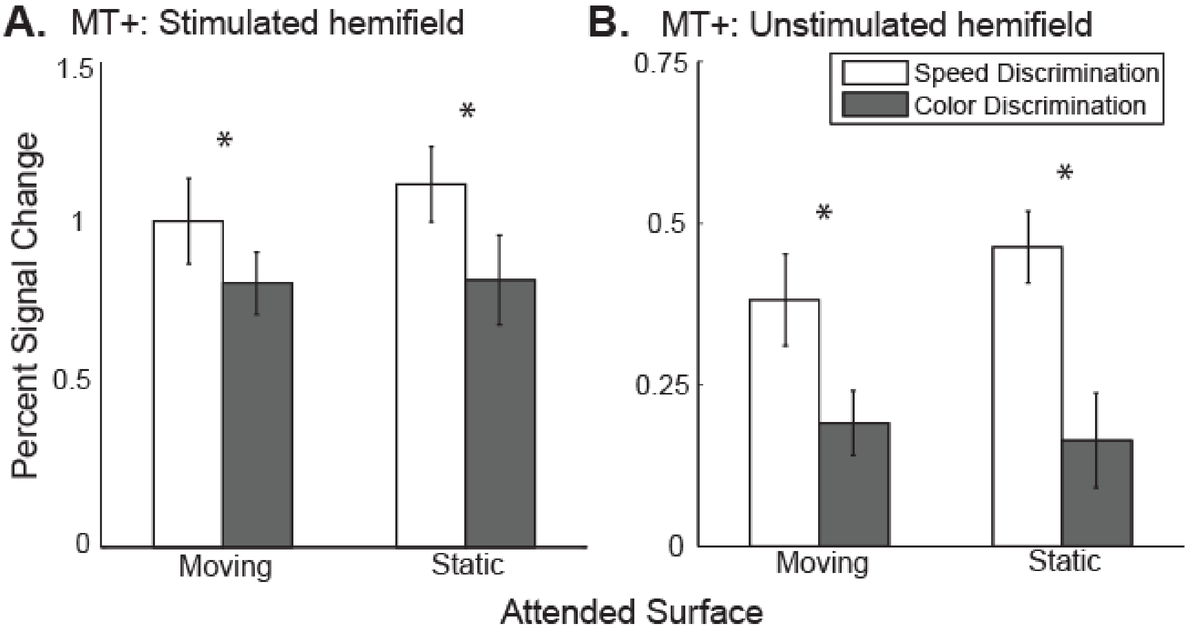

Figure 4. A) Experiment 1. Percent signal change (from pre-block fixation baseline) in MT+ (stimulated hemisphere), averaged across six observers during speed discrimination (white) and color discrimination (gray) while attending to the moving surface or to the static surface; error bars represent one standard error of the mean. B) Same conventions as in A, but representing MT+ in the unstimulated hemisphere. The effect of task was significant in both the stimulated and unstimulated hemispheres (see text). Asterisks indicate significant effect of task within attend-surface conditions ($p < .05$).

was motion present?), whereas it is a discrimination task in the other three conditions. The overall task-driven response pattern, regardless of which surface was attended, was largely consistent across observers, despite some variability in overall signal change magnitude. Interestingly, MT+ showed a similar pattern of responses in the *unstimulated* hemisphere as in the stimulated hemisphere (figure 4b): we analyzed the data from MT+ when observers were attending to a stimulus isolated to the ipsilateral visual field, and found a significant effect of task ($p < .0005$, $n = 6$), and no effect of attended surface. The only reliable difference between the stimulated and unstimulated hemispheres was in terms of overall signal change magnitude.

We expected to find the complementary task-dependency in area V4 (color discrimination > speed discrimination). Corbetta et al. (1991) found foci of activation in an area roughly corresponding to V4 when observers performed a color discrimination task. In our experiment, all the ROIs were defined by finding the intersection between retinotopic areas and the most significant voxels using the motion > static localizer contrast. This was done to restrict the data to the areas of visual cortex corresponding to the stimulated region of the visual field. We performed a second localizer contrast (chromatic > isoluminant gray) that isolated color-selective voxels located on the ventral surface of the occipital cortex, which corresponded to a contiguous subregion of V4. We analyzed the data restricted to these explicitly color-selective voxels, and found a trend towards a similar activation pattern as MT+, but with the complimentary task-dependency (color > speed – figure 5). This trend was nearly significant ($p = .056$, $n = 4$) in the stimulated hemisphere. The localizer contrast was reliable in only four out of the six observers, and the analysis was restricted to those four. The results of Experiment 1 indicate that task is the primary factor modulating the responses in MT+ and V4 and that the physical properties of the attended stimulus have little or no effect. This raises the question of

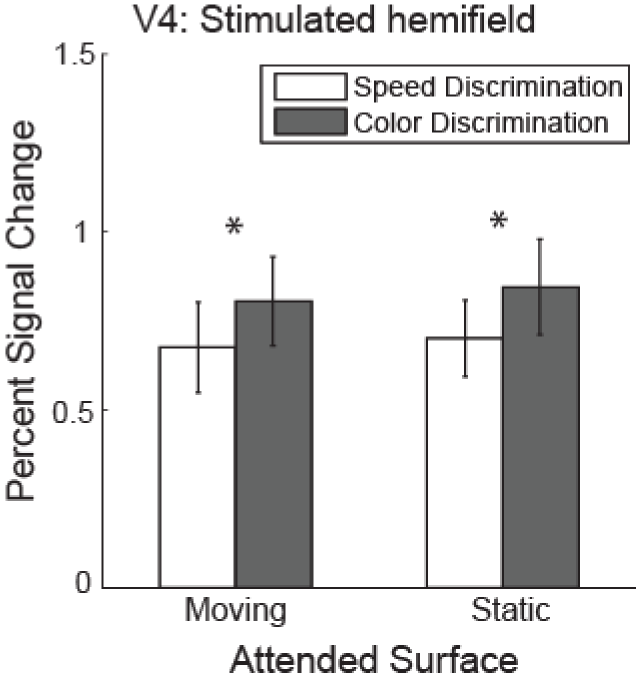

Figure 5. Experiment 1. Percent signal change in V4 (stimulated hemisphere), averaged across four observers, when the ROI was restricted to the voxels selected by a color-selective contrast. Conventions are the same as in figure 3. The effect of task was significant in (see text). Asterisks indicate significant effect of task within attend-surface conditions (p < .05).

whether task and stimulus properties are completely independent factors or interact in some way. To address this question we designed experiment 2 to have multiple levels of stimulus density – including no stimulus. It is possible that preparing for a particular discrimination task – in the absence of any stimulus – may change responses in a similar manner as the act of actually performing the task. Chawla et al. (1999) found increases in the response of areas MT+ and V4 when a preferred stimulus feature (speed, color) was cued for discrimination, relative to a non-preferred feature; similar effects were found by Puri et al. (2009) in the fusiform face area and the parahippocampal place area for faces and places, respectively, and by Giesbrecht et al. (2006) for color and location. However, Shulman et al. (2002) did not find any differential effects between cueing for a color- or motion-discrimination task within any region of occipital cortex during a preparatory period, but did find differential effects within MT+ during the subsequent discrimination period. A more recent study also failed to find any effects of preparing for a color or motion task (McMains et al. 2007). Given the ambiguous nature of previous results, we cannot determine the extent to which the task-driven modulations found in

Experiment 1 and in previous studies were due to anticipation effects, and to what extent they were dependent on stimulation. Experiment 2 was designed to address this possibility – using an event-related design with 12 different conditions, independently varying stimulus density, attended side, and task.

EXPERIMENT 2:

METHODS

Subjects

Seven observers were included in Experiment 2 (four males), ranging in age from 24 to 31. Four of the observers also participated in Experiment 1, one of whom was author ER. All subjects again gave written and informed consent in accord with the human subjects Institutional Review Board at the University of Washington, had normal or corrected-to-normal vision, and were compensated $20/hr. As in Experiment 1, each observer took part in two one-hour sessions in the lab for practicing the experimental conditions, two one-hour psychophysics sessions in the scanner, and two scanning sessions. Both sessions contained a mix of experimental, retinotopic mapping, and localizer scans. Data from one of the seven observers was excluded from analyses due to unreliable region-of-interest definitions.

Stimuli

Within each quadrant of the visual field, an identical number of limited-lifetime moving dots occupied a circular aperture (five degrees diameter, centered seven degrees to the left/right of fixation, four degrees above/below fixation; figure 6A). Each dot occupied 0.25 degrees of visual angle, and was randomly replotted every 100 frames or when it exceeded the aperture bounds. The color (reddish) and speed (average: 4.5 deg/sec) of the dots within each aperture was identical, but varied between apertures. In all phases of the experiment, the dots moved upwards.

Display apparatus

The machines and monitors used in the various phases of Experiment 2 were the same as those used in Experiment 1.

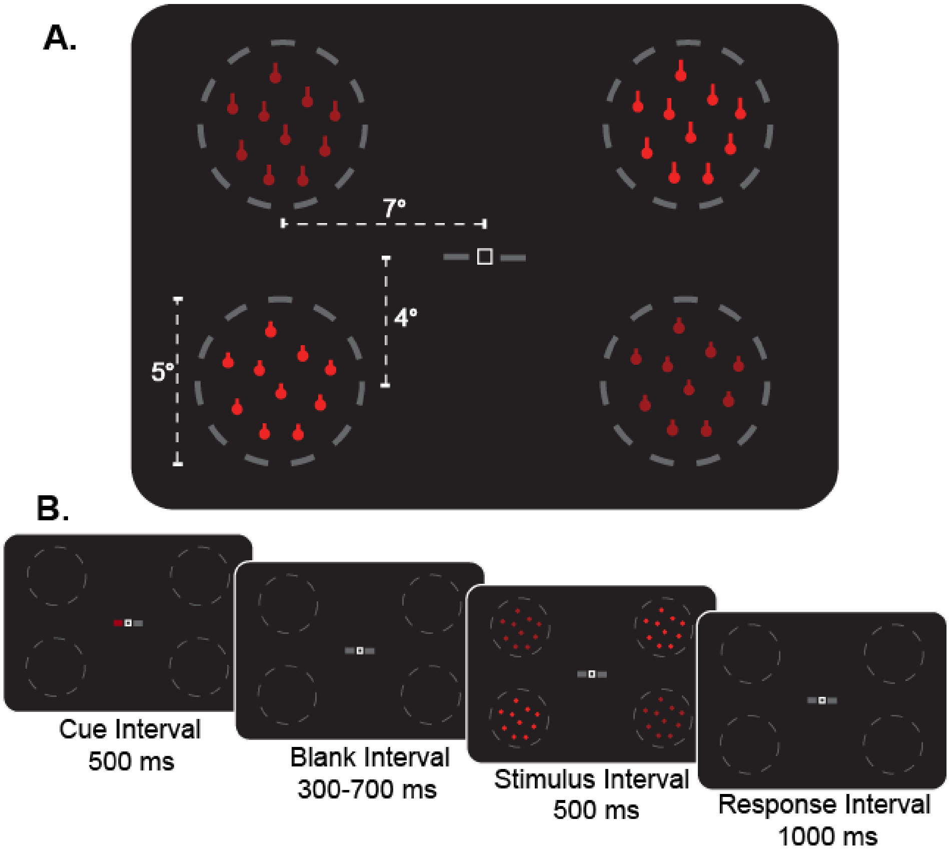

Figure 6. A) Schematic of stimulus used during Experiment 2. The color and speed of the dots within each aperture varied independently across trials. Dashed gray circles depict the extent of stimulus apertures (not present during the experiment). This schematic depicts the stimulus during the high-density condition (10 dots per aperture). B) Procedure for a stimulus-present trial – Exp. 2. In this example, the cue period directs the observer to attend to the color (red cue) of the dots in the apertures to the left of fixation. During blank trials, no cue was given, and no stimulus appeared (fMRI sessions and practice only). During threshold estimation trials, observers reported which aperture on the attended side contained either the fastest dots or the dots that were chromatically more red. During scanning, observers reported whether the apertures on the attended side appeared identical or different on the attended dimension.

Procedures

Practice: Each observer began the experiment by participating in a one-hour practice session in the lab, intended to produce familiarity with the task and to estimate appropriate initial parameters for a staircased threshold-estimation procedure later completed in the scanner.

During the imaging phase, there were twelve main conditions. These were products of three independent variables (stimulus density – 3 levels; task – 2 levels; spatial attention – 2 levels). On a given trial, each quadrant aperture contained zero, three, or 10 dots, while observers performed either a speed or color discrimination task between the two apertures in either the left or right visual field. The observers' task was to determine which of the two apertures contained dots moving at a higher velocity (speed task) or appeared more reddish (color task). The zero-dot conditions were not included during practice or threshold measurements. Figure 6b outlines the procedure for a given trial.

Practice consisted of eight blocks of 80 trials each (one block per condition), during which observers performed the appropriate discrimination task. Each trial began with a 500 ms cue interval, separated from a single stimulus interval by 300-700 ms (randomly varied so that stimulus onset could not be predicted). The stimulus appeared on the screen for 750 ms, and was followed by a 1000 ms response window. Observers indicated which aperture on the attended side contained either the fastest moving dots (if performing speed discrimination) or the dots with the most reddish hue (if performing color discrimination). Feedback was given, and the difficulty of the next trial was determined by a three-down one-up staircase. The intertrial interval lasted, on average, 1250 ms. The magnitude of the between-aperture difference in the untracked dimension on the attended side was kept similar to the magnitude of the attended dimension on a trial-by-trial basis; both dimensions in the unattended hemifield were modulated in a similar fashion. The 'correct' aperture on each trial was independent between hemifields and feature dimensions, such that if the observer was performing the wrong task or attending to the wrong hemifield, performance would be at chance (50%).

Psychophysical threshold measurements: As explained in Experiment 1, it was important to equate the difficulty of the various task conditions. To this end, we again estimated the difference increment on each dimension that yielded threshold accuracy. Observers completed blocks of single-condition trials while lying in the bore of the scanner, and responded using a fiber-optic key-press device. The initial values for each staircase were loosely based on performance during the practice session. The procedure was otherwise identical to the lab practice. As in Experiment 1, Weibull functions were fit to the data using a maximum likelihood procedure to estimate the speed or color difference that would produce 79% correct performance during each block of trials. These threshold differences were then averaged across visual fields, and implemented in the experimental fMRI session.

Practice - fMRI task: On a separate day before scanning, each participant spent about one hour in the lab practicing the fMRI version, until performance on each condition was reliably above chance and the participant felt comfortable with the procedure. The fMRI experiment differed from the psychophysical sessions in several ways. First, the task on each trial during imaging was to decide whether the two stimuli in the attended hemifield were the same or different in the attended dimension. Second, the magnitude of any color or speed differences between apertures was determined by the estimated psychophysical thresholds, and remained constant across trials and scans. Third, an event-related design was used in which every trial type was interleaved during a single scan. For analysis purposes, it was also necessary to include blank trials, during which only the fixation mark remained on the screen, and no attention-directing cue appeared. Finally, participants did not receive feedback after responding.

fMRI sessions: Each participant took part in two fMRI sessions over two separate days. On the first day, four event-related scans were administered, along with two spot localizer scans. The event-related scans contained multiple repetitions of the 12 unique conditions described above, along with blank trials, presented in sequences designed for efficiency in the timeseries deconvolution procedure described below. Each event-related scan contained 128 trials (32 blank trials, eight repetitions of each of the 12 conditions), and followed the sequence outlined in figure 6b. On each trial, the participant foveated the fixation mark, followed the instructions provided by the attention cue (red left arrow: attend left, color task; red right arrow: attend right, color task; yellow left arrow: attend left, speed task; yellow right arrow: attend right, speed task), viewed the stimulus, and made a response using a magnet-compatible fiber-optic key-press device.

The second session also consisted of four event-related scans, as well as two standard retinotopic mapping scans (rotating wedge & expanding ring). Across the two days, the data from each participant included 64 trials of each condition.

Defining ROIs

The initial fMRI experimental session included two repetitions of the same localizer scan utilized in Experiment 1. The procedures for defining ROIs were identical to those from Experiment 1.

fMRI data acquisition

FMRI data were acquired in the same Phillips 3T scanner using the same sequence and head coil as in Experiment 1. However, the acquisition parameters were slightly different. Data were acquired with a repetition time of 1 s and echo time of 22 ms. Eighteen axial slices (64 × 64 matrix, 220-mm field-of-view, no gap) were collected per volume (voxel size: 3.4 x 2.75 x 2.75 mm). Preprocessing steps were performed using BrainVoyager, and custom Matlab code used for subsequent analyses. Time series were low-pass filtered, and normalized by subtracting and dividing by the mean.

fMRI data analysis

For each scan separately, hemodynamic responses (HDR) to each of the 12 conditions were estimated by deconvolving the timecourse by the pseudo-inverse of the design matrix (Dale 1999). We chose not to pre-whiten the time-series prior to deconvolution because we found that the remaining temporal autocorrelations after low-pass filtering were minimal, and that the choice of method for pre-whitening can have significant effects on the results. Since our design matrix was counterbalanced, we do not expect any remaining temporal autocorrelations to cause any systematic biases in our estimated responses across conditions.

The peak response of each HDR was calculated for each scan, visual area, and participant by averaging timepoints 5 and 6 following the onset of the attention cue. We were mainly interested in the initial part of the estimated response, because each subsequent time point would be increasingly contaminated by subsequent trials. Across conditions, the estimated HDRs were indistinguishable beyond time point 6. This procedure was carried out separately for voxels in the two hemispheres. For each participant, the peak responses were then averaged across scans to yield one summary point per ROI and condition. We averaged the summary points across participants to yield grand means. Each hemisphere was considered separately.

Eye tracking

No eye tracking was performed during Experiment 2. We intended to collect fixation data, but technical issues prevented us from doing so. However, the absence of significant fixation biases during Experiment 1 alleviates, to some degree, any concerns about fixation biases playing a role in the outcome of Experiment 2. The same observers whose fixation data was analyzed in Experiment 1 were used in Experiment 2, and the procedures were fairly similar across the two experiments.

RESULTS

Behavioral performance: Behavioral performance in Experiment 1 was not significantly different between conditions, and was always around 80%. In Experiment 2, however, this was not the case. Performance was in general higher during speed discrimination than during color discrimination (grand means: 72.8%, 62.5%). Five of six observers performed well below 80% on all four conditions. Four of six performed at least 10% better on their 'best' condition than on their 'worst' condition, and two of six had a disparity of at least 20%. Percent correct on the four conditions for all observers, collapsed across attended side, is represented in Table 3.

	Attend Color		Attend Speed	
Subject	3 dots	10 dots	3 dots	10 dots
S1	58.5% (10)	56.9% (3)	68.1% (10.8)	62.2% (9.6)
S2	60.0% (10)	68.4% (8)	62.1% (32.1)	77.9% (31.3)
S3	49.7% (10)	55.2% (3)	78.6% (20.1)	65.6% (20.3)
S4	63.3% (9)	52.3% (3)	65.6% (20.6)	77.1% (15.4)
S5	73.2% (12)	55.4% (9)	79.7% (31.6)	67.2% (27.5)
S6	81.1% (9)	76.5% (8)	84.9% (21.0)	84.9% (13.1)

Table 3. Values are percent correct on the four main conditions for which responses were required, averaged across hemifields. "Attend Color" columns: performance during color discrimination conditions; "Attend Speed" columns: performance during speed discrimination conditions; "3 dots" columns: performance during low-density stimulus conditions; "10 dots" columns: performance during high-density stimulus conditions. Discrimination thresholds are provided within parentheses (speed discrimination: deg/sec; color discrimination: RGB increments)

During scanning, responses were based on whether or not the stimuli within the two apertures were the same or different in the relevant dimension. However, during threshold estimation, responses were two-alternative forced-choice, based on which aperture on the attended side contained either the fastest dots or the chromatically more red dots, depending on task (because thresholds are much easier to derive with 2AFC trials). This change, and the fact that no behavioral feedback was given during scanning, very likely explains why performance deviated from 80%, despite administering at least one hour of practice on the scanner task in the lab shortly before scanning. Given that the goal was to control for task difficulty as a general confound, it was possible that the imaging results could have been in some way biased by the differential levels of performance across the conditions. To analyze whether or not this was likely, we computed the correlation between percent correct and BOLD percent signal change (24 data points: four conditions, six observers), and found that the latter could not be predicted by the former in any of our ROIs. Thus, we have no strong reason to suspect that differences in behavioral performance produced spurious differences in BOLD responses.

fMRI responses - Effects of task: In Experiment 1, we found a significant main effect of task in area MT+ in the hemisphere representing the attended visual field (‘attended data’), as well as in the hemisphere representing the unattended visual field (‘unattended data’). When participants performed a speed-discrimination task, responses were higher than when they performed a color-discrimination task. The results from Experiment 2 for MT+, averaged across participants, are shown in figure 7 (a, b). As in experiment 1, we found that fMRI responses in area MT+ were larger during the speed discrimination task than for the color discrimination task, but only for the 3 and 10 dot conditions (separate t-tests conducted for each stimulus density condition: (0 dots: $p = .771$; 3 dots: $p = .015$; 10 dots: $p = .028$). There was no overall main effect for task in area MT+, presumably because of the null-result for the zero dot condition (main effect for task: $p = .07$, 2WRM ANOVA). There was also no significant interaction between task and stimulus density, but somewhat surprisingly, the main effect of task from responses to the unattended stimulus was highly significant in MT+ (*p* < .001, 2WRM ANOVA), but was also dependent on stimulation (0 dots: *p* = .596; 3 dots: *p* = .003; 10 dots: *p* = .032).

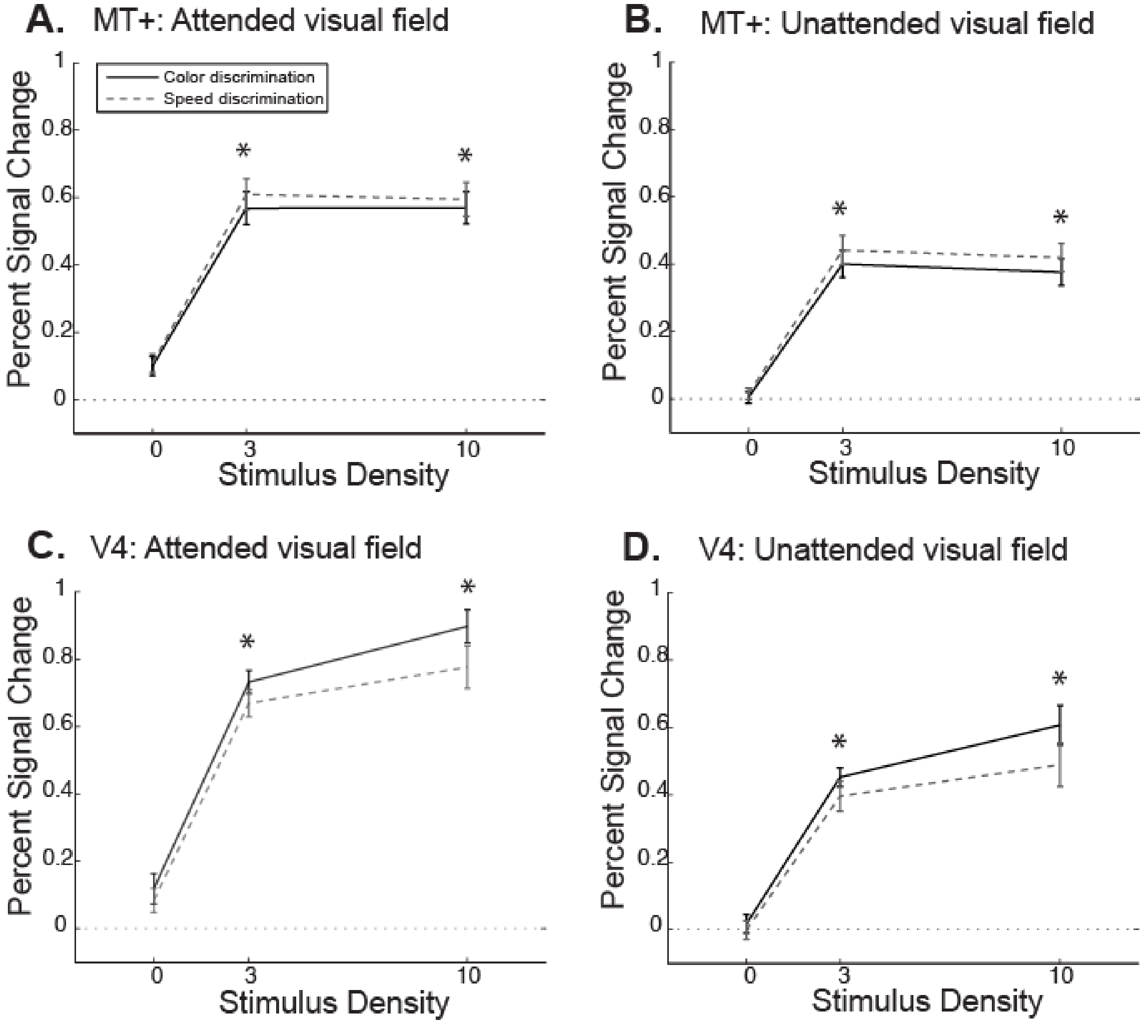

Figure 7. A) Experiment 2. Average fMRI responses across six observers in MT+ (A: attended visual field, B: unattended visual field) and V4 (C: attended visual field, D: unattended visual field) while performing speed discrimination (dashed gray) and color discrimination (black). Stimulus density is in terms of number of dots within one aperture. Error bars represent one standard error of the mean. Asterisks indicate significant effects of task at individual stimulus densities (p < .05).

We found a trend towards significance in the color-selective voxels (subregion of V4) in Experiment 1 as a function of task (color > speed, fig. 5). In Experiment 2, we once again defined voxels within V4 that were color-selective on the basis that they responded more to a chromatic field of dots than to an isoluminant gray field of dots (figure 7c, d). The main effect of task was significant in the attended data (*p* = .035, 2WRM ANOVA), but as in MT+, depended on the presence of a stimulus (0 dots: *p* = .126; 3 dots: *p* = .009; 10 dots: *p* = .010). There was a trend towards significance from the unattended stimulus (*p* = .059, 2WRM ANOVA), and a significant effect during the high-density condition (0 dots: *p* = .684; 3 dots: *p* = .093; 10 dots: *p* = .006).

As in Experiment 1, there were no effects of task in any of the other ROIs that we analyzed. V1, V2, and V3 were not modulated by task at any stimulation level, whether considered separately or as one homogenous ROI.

fMRI responses - Effects of spatial attention: We calculated main effects of spatial by subtracting the mean percent signal change across all three stimulation conditions and the two task conditions in the hemisphere representing the unattended hemifield from the mean percent signal change in the attended hemifield. The effects of spatial attention were robust, showing significant modulations in all ROIs (V1: *p* = .013, V2: *p* = .05, V3: *p* = .006, V4: *p* = .01, MT+: *p* < .001). Percent signal change for the attended and unattended conditions is plotted in figure 8.

Scrutiny of figure 8 reveals two interesting findings. First, the effect of spatial attention appears to be well-represented by a simple baseline shift when a stimulus is present – the increase in percent signal change was the same for the 3- and 10-dot conditions. This is consistent with previous studies investigating the effect of spatial attention as a function of stimulus contrast (Murray 2008; Buracas and Boynton 2007). Second, the effect of spatial attention was considerably smaller when no stimulus was presented, indicating that spatial attention might interact with stimulation. This interpretation would not be compatible with an additive baseline shift model, but the 0-dot condition differed from the 3- and 10-dot conditions in other ways that may explain the discrepancy (see Discussion).

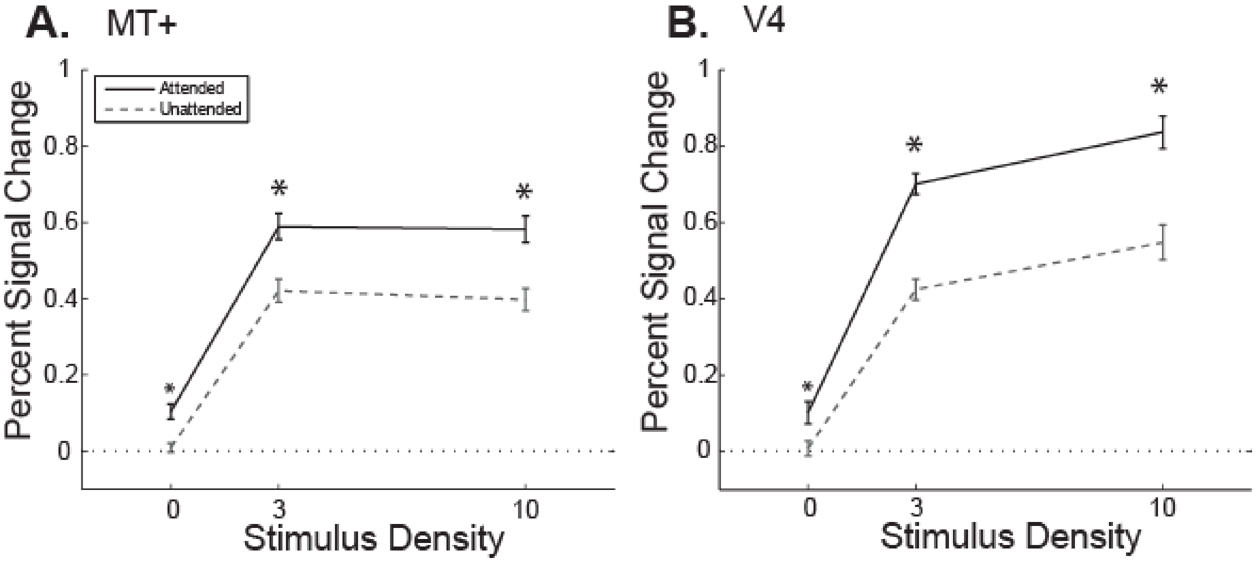

Figure 8. Experiment 2. Effect of spatial attention. A) MT+, averaged across six observers; solid black curve: average percent signal change across the two task conditions in the hemisphere representing the attended visual field; dashed gray curve: data from hemisphere representing the unattended visual field. B) same conventions as in A, but for V4 (four observers). Error bars represent one standard error of the mean. Asterisks indicate significant effects of task at individual stimulus densities ($p < .01$).

We further subdivided the data by analyzing the effect of spatial attention for each task condition separately. Figure 9 shows the effects of spatial attention as a function of task and stimulus density for areas MT+ (A) and V4 (B). It is apparent from these plots that the effect of spatial attention is independent of what task is being performed, and of stimulation level.

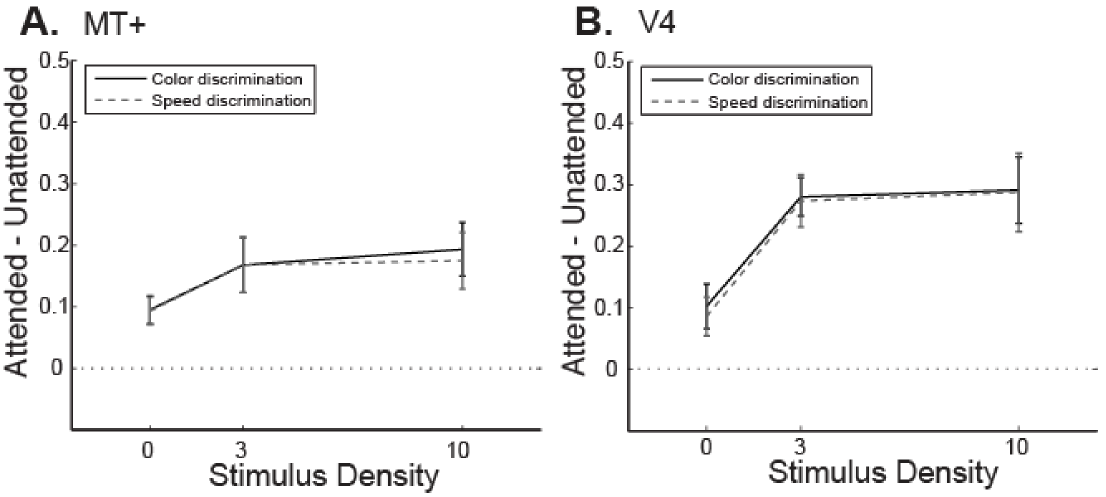

Figure 9. Experiment 2. No differential effect of spatial attention as a function of task. A) MT+, averaged across six observers; the curves represent the difference, for each task condition, between the data obtained from the attended visual field and the unattended visual field. Solid black curve: the difference between the solid black curve in figure 7b and the solid black curve in figure 7a. Dashed gray curve: the difference between the dashed gray curve in figure 7b and the dashed gray curve in figure 7a B) Same conventions as A, but for V4, averaged across four observers (solid black curve: the difference between the solid black curve in figure 7d and the solid black curve in figure 7c). Error bars represent one standard error of the mean difference.

DISCUSSION

Task-driven modulation: The results of Experiment 1 replicate previous findings showing that task can modulate population-level responses in visual cortex (Corbetta et al. 1990, 1991; Beauchamp et al. 1997; Chawla et al. 1999; Huk and Heeger 2000). Specifically, the responses of populations containing a large proportion of neurons tuned to a particular feature (motion, color) increase when that feature is task-relevant compared to when it is not. We found an increase in BOLD response in MT+ during speed discrimination blocks relative to color discrimination blocks, and the complementary effect in color-selective voxels within V4. No significant modulation by task was found in areas V1, V2, V3, or V3A. Task-dependent modulation was also found in voxels representing the opposite visual hemifield (MT+), suggesting the operation of a feature-based gain mechanism that increases the responses of neurons tuned to a task-relevant feature, regardless of receptive field location (Treue and Martinez-Trujillo 1999; Saenz et al. 2002). This result corroborates that of Serences and Boynton (2007), who were able to classify the attended direction of motion presented in one visual hemifield based on responses to the other, unstimulated, hemifield. The importance of task in modulating the responses of specific neural populations was largely replicated in Experiment 2, which also provided additional information about the timing of the effect. In Experiment 1, tasks were performed in 20-second blocks; thus, the data did not provide information about the timecourse of task-related modulation. It is possible that multiple trials were necessary for task-related signals to appear after switching from performing a block of one particular task to performing another. The well-documented detrimental effects of task switching on behavior support this possibility: the first trial after switching tasks almost always produces reduced performance, even with long intertrial intervals (Sohn et al. 2000; Monsell 2003). The event-related design of Experiment 2, where tasks were interleaved, produced task-driven modulation regardless of frequent task switching, suggesting that task-related signals manifest more quickly than could be discerned by Experiment 1. This result is consistent with those of Liu et al. (2003), who demonstrated rapid modulation differences in feature-selective sensory areas when attention was cued to 'hold' on a currently attended preferred feature versus when attention was cued to 'hold' on a non-preferred feature. One previous study failed to find any effects of task on responses in visual cortex (Buracas et al. 2005). We speculate that the discrepancies between that study and our findings (and other studies showing similar effects) are due to methodological differences. First, Buracas et al. (2005) compared the effects of performing a speed discrimination task to those of performing a contrast discrimination task. If, as our results suggest, performing a task requiring information about a specific feature increases the response of neurons tuned to that feature, then performing a contrast discrimination task may not modulate responses at all, since contrast might be thought of as a measure of stimulus intensity rather than a feature. Individual neurons display preferential tuning for stimulus attributes such as orientation, direction of motion, and spatial frequency. However, this is not the case for contrast; increasing contrast typically yields monotonically increasing neuronal responses. Second, Buracas et al. (2005) used a moving grating stimulus, containing only a single spatial frequency, whereas a moving field of dots contains a wide range of spatial frequencies (the Fourier spectrum of a point includes energy at all frequencies). Thus, it is likely that our stimulus activated more neurons in general, leading to a larger signal-to-noise in the population average response. Combined, these two factors could have led to the cloaking of a real effect of task in Buracas et al. (2005).

What are the possible neural mechanisms involved in instantiating the observed task-driven modulations in MT+ and V4? The most commonly proposed explanation is that a general response gain is applied to neurons selective for a task-relevant direction of motion (in the case of motion tasks). This response gain could also be accompanied by an increase in selectivity for task-relevant features. Serences and Saproo (2010) measured voxel-based tuning functions for orientation in early visual cortex as they varied the relative value of oriented gratings presented in the left and right visual fields. They found a sharpening of tuning functions in voxels tuned to one of the orientations when that stimulus became valuable (monetary reward for responding to the correct orientation). It is possible that such a mechanism contributes to the task-driven modulations observed here; as different features become 'valuable,' or task-relevant, neurons tuned to those features may sharpen their response profiles, allowing for increased discrimination sensitivity between directions of motion and colors (Shadlen et al. 1996; Serences et al. 2009).

The role of stimulus properties: O'Craven et al. (1997) found that responses in MT+ modulated as a function of surface selection. When attention was directed to a moving surface, responses were strongly increased relative to when observers attended to a static surface. However, we found no such effect in MT+ (nor in any of the ROIs), even though the voxels were defined on the basis of being strongly modulated by a moving stimulus relative to a static stimulus. This discrepancy could be due to the absence of a task in the O'Craven study; observers were simply instructed to 'attend' to one of the surfaces. In the absence of a controlled task, there are no grounds for ruling out the possibility that observers were simply more aroused or engaged with the stimulus when attending to the moving surface. The static stimulus in Experiment 1 did contain a threshold-level amount of horizontal motion during some intervals; it could be argued that the equality of the selection conditions within a given task condition was due to motion energy being present in both surfaces. However, a pilot experiment performed in our lab (unpublished) with the same conditions and procedure as in Experiment 1 (except the motion task/attend static condition) used a truly static surface (no small increments – as in Experiment 1), and revealed that responses in MT+ did not depend on which surface was attended when a color task was performed – the responses were equal. These results indicate that the modulatory effect of task does not necessarily depend on the physical properties of the selected stimulus. It should be noted, however, that the stimulus used by O'Craven et al. was centered at fixation, and had a lower overall density of dots than the stimuli used in our Experiment 1 (0.48 dots/deg^2 versus 2.65 dots/deg^2). These factors may have allowed subjects in their experiment to attend more selectively to one field over the other. However, we believe this explanation to be unlikely, as the high performance of our subjects indicate that they had no problem selecting the relevant stimulus.

Based on previous research it is unclear whether there are response increases (e.g., in MT) when a preferred stimulus (e.g., motion) is anticipated. Chawla et al. (1999), Giesbrecht et al (2006), and Puri et al. (2009) demonstrated response increase during cue periods in areas tuned to the cued feature. However, neither Shulman et al. (2002), nor McMains et al. (2007) found any such modulations. Our Experiment 2 suggests that the presence of a relevant stimulus might be necessary for task-driven modulation of population responses. The effect of task was only significant during conditions when a stimulus was presented on the screen. Although each trial was preceded by a cue indicating the task to be performed (except blank trials), cue-driven processing was not by itself sufficient to modulate responses. However, the 0-dot conditions also did not require a decision or a response. Therefore, we cannot rule out the possibility that task-specific decision-response processes play more or less of a role in modulating responses than stimulation. As the results stand, it is safe to say that some combination of stimulation, decision, and response are necessary for task-driven modulation, and not cue-driven signals related to preparing the neuronal circuitry for a particular task. Further studies are necessary to differentiate the relative importance of stimulation, decision, and response.

Spatial attention, task, and stimulation:

The design of Experiment 2 allowed us to investigate whether the effect of spatial attention is dependent on either task, stimulation density, or some combination of the two. Previous imaging studies have demonstrated that attending to a region of visual space increases the response of voxels selective for that region, independent of stimulus contrast (Murray 2008; Buracas and Boynton 2007). This is suggestive of a baseline shift in the responses of the underlying neurons tuned to the attended space, applied after any stimulus-related processing and multiplicative gain modulations (Boynton 2009; Boynton 2011). Our results are consistent with a baseline shift when a stimulus was present: responses to the attended side were larger than responses to the unattended side by the same amount regardless of whether a 3- or 10-dot stimulus was presented, in all ROIs. However, when no stimulus was presented, the difference was much smaller. Interpretation of this result is complicated by differences between the 0-dot conditions and the 3- and 10-dot conditions. First of all, there was no stimulus in the former case, and therefore – again – no decision and response were necessary. Consequently, there was less incentive for observers to maintain spatial attention at the cued location, instead of simply returning it to fixation in anticipation of the next cue (even though they were explicitly instructed to keep attention on the attended side until the next cue appeared). If observers were inconsistently attending, the apparent stimulus-dependency would likely have been produced.

Therefore, we cannot rule out that the results are indeed consistent with previous studies showing a stimulus-independent baseline shift in responses from spatial attention.

The effect of spatial attention also appears to be independent of which task is being performed. The difference in response between the attended hemisphere and the unattended hemisphere did not vary with the two tasks implemented in Experiment 2, even though performance was considerably higher during speed-discrimination than during color-discrimination trials (grand means: 72.8%, 62.5%, Table 3).

In this study we have measured the effects of attentional processes using only the BOLD signal, and have assumed that increases in BOLD are coupled to increases in neural responses directly involved in attentional modulation (by task and spatial attention). However, a recent study that separately measured BOLD along with cerebral blood flow (CBF) found that CBF might be a more sensitive index of top-down attentional modulation than BOLD (Moradi et al. 2012). The authors found that directing attention to a visual stimulus in a peripheral location modulated the CBF response about twice as much as the BOLD response, relative to when the same stimulus was unattended. More research is necessary to understand the full relationship between attention, CBF, and neural activity, but it may be that relatively small top-down effects such as those observed here would be more robustly detectable using CBF as an index.

Conclusions: We can say with confidence that performing different tasks requiring different visual information systematically modulates responses across visual cortex. Specifically, our results are consistent with previous findings that a motion-related task increases responses in MT+ and a color-related task increases responses in V4. In general, it is likely that populations containing a large proportion of motion-tuned neurons are modulated by a motion-task, and vice versa for color. However, motion-tuned populations (specifically MT+) do not seem to be modulated when attention selects a stimulus containing motion that is superimposed on a stimulus that is static, contrary to previous reports (O'Craven et al. 1997). Although our results suggest the possibility that stimulation might be necessary for task-driven modulation, rather than the act of task-anticipation, limitations inherent in our method prevent us from making any strong conclusions regarding this point. Similarly, although spatial attention increased responses by a larger amount when a stimulus was present than when absent, we cannot rule out that the results are consistent with a baseline shift of attention, especially since the effect was independent of stimulation when a stimulus was presented. However, it is clear that spatial attention does not interact with what task is being performed, suggesting that the neural mechanisms involved are independent. In sum, the results of this study indicate that manipulating stimulus density, task type, and spatial attention produce patterns of responses in MT+ and V4 that are largely independent from each other. We are not aware of any previous studies demonstrating separability of these modulations.

Summary

In Chapter 1, I explored the effects of divided attention on physiological responses in primary visual cortex. Previous fMRI studies found strong effects of divided attention to relatively complex stimuli, such as letters and feature-conjunctions, and/or implementing tasks such as change detection. Such experimental features have shown to produce behavioral performance indicative of limited capacity processing (Shaw, 1984; Harris et al., 2004; Scott-Brown and Orbach, 1998). In contrast, unlimited capacity processing have been found when observers perform visual search for a predefined and constant target, and when the relevant stimuli are composed of simple features, such as oriented gratings or contrast patches (Huang and Pashler, 2005; Scharff et al., 2011). Will the BOLD signal measured from V1 still show effects of divided attention under such circumstances?

The findings presented in Chapter 1 suggest that there are situations which allow attention to be spread across multiple spatial locations without reducing the neural resources available for representing each individual source in primary visual cortex. Contrary to previous fMRI studies, I found no BOLD signal reduction during divided attention relative to focused attention. Recently, Chen and Seidemann (2012) found a similar null result using optical imaging in monkeys. As noted in the discussion of Chapter 1, we hypothesize that the discrepant results stem from two factors: stimuli defined by simple features catered to the tuning properties of a large proportion of neurons contained within primary visual cortex, and the use of a visual search task with a constant target.

This hypothesis leads to some testable predictions. First of all, the same experiment can be carried out again using a more complex class of stimulus, such as words or objects masked by noise. Additionally, task complexity can be manipulated by varying the target stimulus from trial to trial, or by asking observers to detect an identity change across relevant location(s) within a trial. If our hypothesis is correct, these types of manipulations should reduce the BOLD signal during divided attention relative to focused selective attention. Future imaging studies on divided attention should vary these factors.

Chapter 2 investigated the independent and combined effects of attentional selection, task type, and spatial attention on the responses of different neural populations within early visual cortex. As noted in the introduction, attention can be used to select between spatially superimposed surfaces composed of different stimulus properties, such as motion and color. Selection of a moving surface has been shown to increase physiological responses in MT+, an area composed primarily of neurons responsive to motion. Likewise, selection of a colored surface increases responses in V4. Another aspect of selection involves the task used to engage attention on the appropriate stimulus; experimentally, it is not possible to ensure that an observer is correctly attending without collecting behavioral responses. It turns out that the type of task used to engage an observer’s attention can differentially modulate responses across areas of visual cortex. For example, responses in MT+ have been shown to modulate when switching between analyzing the motion properties and the color properties of a constant stimulus (Corbetta et al., 1990, 1991; Beauchamp et al., 1997). I performed a study composed of two experiments seeking to unravel the contributions of these factors on the BOLD signal in human visual cortex; specifically, I investigated 1), the physical attributes of the stimulus being selected, 2), the type of task used to assert selection, and 3), the effect of spatial attention, and 4), any interactions between the factors.

The results strongly suggest that these factors affect BOLD responses across visual cortex in an independent manner. First, I replicated the results of previous studies showing that task can modulate responses across visual cortex systematically. Areas known to be composed of proportionately more neurons responsive to motion than to color yield stronger population BOLD responses during motion-related tasks than during color-related tasks (MT+), and vice versa (V4). Second, these results did not depend on the tested stimulus-related manipulations – as long as a stimulus was present for analysis. The effect was the same regardless of which surface was selected (Experiment 1), or the density of the surface (Experiment 2). Moreover, both left and right MT+ showed just as strong of an effect of task, regardless of which hemifield was being stimulated. Third, the effect of spatial attention did not differ between tasks in any visual area. In Experiment 2, I found no difference in the effect of spatial attention across the tested levels of stimulus density, consistent with previous studies (e.g. Murray, 2008; Buracas and Boynton, 2007).

There is more to learn about the effects of task on population responses. Specifically, it is unclear whether the observed modulations within MT+ and V4 were as a result of response enhancement, suppression, or a combination of the two. To this end, it would be informative to include a third task condition that invokes neither the analysis of motion, nor the analysis of color, to gain more insight into the effects of analyzing a ‘preferred’ feature within different populations. Also, the origin of the task-driven signals is impossible to discern. Are the modulations of MT+ and V4 produced via feedforward signals already present in V1 responses, or are they produced via feedback from higher-level areas involved in decision making?

The explorations of attention-related phenomena reported in this dissertation share the common theme of controlling attention via different tasks, which presumably engage different populations of neurons in different computational strategies. One of the premises and main intuitions for the work in Chapter 2 is that task-related decisions will be optimal if based on the responses of the most informative neuronal signals, which likely originate in populations with the sharpest tuning for the relevant stimulus attributes. MT+ and V4 are likely to contain neural substrates directly involved in motion discrimination and color discrimination, respectively. In Chapter 1, the finding of unlimited capacity processing in V1 might similarly reflect the possibility that neural responses in V1 are directly involved in the performance of tasks such as detecting oriented gratings, or other such stimuli for which strong tuning exists. This presents another testable hypothesis.

From this work, my colleagues and I have contributed important knowledge about some of the various effects of attention-related processes on physiological responses in the human visual system. In Chapter 1, we demonstrate what we believe to be the first evidence of unlimited capacity processing in human V1 during divided attention, extending the work of Chen and Seidemann (2012) and building on the existing fMRI literature on the topic. The results of Chapter 2 indicate that manipulating stimulus density, task type, and spatial attention produce patterns of responses in visual cortex that are largely independent from each other. Similarly, this is the first study to demonstrate separability of these variables. Although there is still much to be done to understand the attention-related phenomena that are investigated in this dissertation, with this work science hopefully comes a bit closer to the ultimate goal: understanding the physiological links between sensation, perception, and behavior.

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