Evidence for unlimited capacity processing of simple features in visual cortex

Alex L. White
University of Washington, Department of Psychology, Seattle, WA, USA

Erik Runeson
University of Washington, Department of Psychology, Seattle, WA, USA

John Palmer
University of Washington, Department of Psychology, Seattle, WA, USA

Zachary R. Ernst
University of Washington, Department of Psychology, Seattle, WA, USA

Geoffrey M. Boynton
University of Washington, Department of Psychology, Seattle, WA, USA

Performance in many visual tasks is impaired when observers attempt to divide spatial attention across multiple visual field locations. Correspondingly, neuronal response magnitudes in visual cortex are often reduced during divided compared with focused spatial attention. This suggests that early visual cortex is the site of capacity limits, where finite processing resources must be divided among attended stimuli. However, behavioral research demonstrates that not all visual tasks suffer such capacity limits: The costs of divided attention are minimal when the task and stimulus are simple, such as when searching for a target defined by orientation or contrast. To date, however, every neuroimaging study of divided attention has used more complex tasks and found large reductions in response magnitude. We bridged that gap by using functional magnetic resonance imaging to measure responses in the human visual cortex during simple feature detection. The first experiment used a visual search task: Observers detected a low-contrast Gabor patch within one or four potentially relevant locations. The second experiment used a dual-task design, in which observers made independent judgments of Gabor presence in patches of dynamic noise at two locations. In both experiments, blood-oxygen level–dependent (BOLD) signals in the retinotopic cortex were significantly lower for ignored than attended stimuli. However, when observers divided attention between multiple stimuli, BOLD signals were not reliably reduced and behavioral performance was unimpaired. These results suggest that processing of simple features in early visual cortex has unlimited capacity.

Introduction

It is generally a bad idea to attend to many things at once. For instance, it would be unwise to drive a car while reading a book. Focusing attention improves your ability to make judgments of relevant stimuli and filter out irrelevant distractions. But is perceptual processing always worse when attention is divided? Behavioral research has in fact identified some tasks that suffer no costs of divided attention, consistent with unlimited capacity parallel processing. Those tasks have not been tested with human neuroimaging, however. The present study bridges that gap by measuring the effects of divided spatial attention on both behavioral and neuronal responses to simple visual stimuli.

We first must distinguish between two related effects of covert, endogenous spatial attention, which we define as the voluntary selection of particular locations without moving the eyes. First, an effect of selective attention is a difference between responses to focally attended and ignored (or less attended) stimuli. For instance, a selective attention effect occurs when observers detect and discriminate information at a cued peripheral location more quickly and accurately than information presented elsewhere in the visual field (e.g., Carrasco, 2011; Kahneman & Treisman, 1984; Palmer & Moore, 2009; Posner, 1980; Shulman, Wilson, & Sheehy, 1985; Yigit-Elliott, Palmer, & Moore, 2011).

Physiologically, selective spatial attention increases the spiking rate of neurons, as well as functional magnetic resonance imaging (fMRI) responses, in areas of cortex that represent the attended location compared with ignored locations (Brefczynski & DeYoe, 1999; Desimone & Duncan, 1995; Gandhi, Heeger, & Boynton, 1999; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Murray, 2008; Tootell et al., 1998; Treue & Maunsell, 1996).

Second, an effect of divided attention is a difference between behavioral or neuronal responses to one focally attended stimulus compared with multiple attended stimuli. Observers can divide attention across multiple relevant locations even when they are non-contiguous (e.g., Awh & Pashler, 2000; McMains & Somers, 2004; Müller, Malinowski, Gruber, & Hillyard, 2003; but see Jans, Peters, & De Weerd, 2010). However, dividing spatial attention often impairs behavioral accuracy and slows response times compared with focused attention (e.g., Braun, 1998; Grubb, White, Heeger, & Carrasco, 2015; Kahneman, 1973; Ling & Carrasco, 2006; Montagna, Pestilli, & Carrasco, 2009). Such costs are especially evident for relatively complex tasks, such as word and object discrimination (e.g., Harris, Pashler, & Coburn, 2004; Shaw, 1984; Scharff, Palmer, & Moore, 2011). A cost of divided attention can be explained by a capacity limit: The perceptual system can process with high fidelity only a limited amount of information per unit time. A related explanation is that finite processing resources must be divided among attended stimuli, leading to impairments. However, some tasks that require merely detecting simple visual features (such as changes in luminance contrast) suffer no costs of divided attention, consistent with unlimited-capacity parallel processing of multiple locations (Bonnel, Stein, & Bertucci, 1992; Graham, Kramer, & Haber, 1985; Scharff et al., 2011).

There have been relatively few studies of the neural correlates of divided attention, and they have all used relatively complex tasks. The few fMRI studies on divided attention in V1 have found blood-oxygen level–dependent (BOLD) signal reductions during divided attention relative to focused attention (McMains & Somers, 2005; N. Müller, Bartelt, Donner, Villringer, & Brandt, 2003; Pestilli, Carrasco, Heeger, & Gardner, 2011). Divided attention also reduces activity in human area V4 under some conditions (Scalf & Beck, 2010). In macaque area V4, neural firing rates are reduced when monkeys attend to two locations compared with just one (Mayo & Maunsell, 2016). Altogether, these experiments support the notion that neural responses are in some way reduced when attention is divided across multiple stimuli, perhaps providing the physiological basis for the capacity limits in similar perceptual tasks. Specifically, the tasks used in those studies were all relatively complex: They required detecting or comparing feature conjunctions or letters, or placed demands on visual working memory to compare multiple stimuli over time.

However, a recent optical imaging study (Chen & Seidemann, 2012) found a striking lack of signal difference in monkey V1 between conditions of focused and divided attention. That study used a yes/no Gabor detection task that was simpler than the previous fMRI studies. As reviewed above, behavioral capacity limitations during divided attention have been found to depend on the complexity of the task and stimuli (Bonnel et al., 1992; Braun, 1998; Braun & Julesz, 1998; Busey & Palmer, 2008; Palmer, 1994; Scharff et al., 2011; Shaw, 1984). Assuming that physiological effects of attention are causally linked to behavioral performance (Ress, Backus, & Heeger, 2000), it follows that the discrepancy between Chen and Seidemann (2012) and other studies of V1 (McMains & Somers, 2005; N. Müller et al. 2003; Pestilli et al., 2011) could be due to differences in tasks and stimuli or to differences in species or imaging method.

To resolve this discrepancy, we conducted the first fMRI study of neuronal responses in early visual cortex when attention is divided across multiple locations during simple visual detection tasks with simple stimuli. By "simple," we mean that the task requires nothing more than reporting the target presence in a single display, and targets can be detected based on a predictable difference from nontargets in just one feature dimension (e.g., orientation). Note that such "simple" tasks can be perceptually challenging if the target's intensity is low.

Our study tested the following hypotheses:

1. When observers are cued to attend selectively to one peripheral location, behavioral and neuronal sensitivity are higher at that location than others.
2. Observers can detect multiple targets defined by simple features in parallel with no cost.
3. Early visual cortex can process multiple simple stimuli with no amplitude reduction during divided attention, compared to focal attention.

Hypotheses 1 and 2 have been supported by previous work, but Hypothesis 3 stands in contrast to previous reports of large divided attention effects in human V1 with more complex stimuli and tasks.

To test the above hypotheses, we conducted two experiments that employed two different paradigms often used to study divided attention: A visual search paradigm and a dual-task paradigm. In both experiments, the task was to report the presence or absence of simple Gabor patches, and we assessed the effect of divided attention by comparing a distributed cue condition with a focal cue condition. However, the two paradigms differed in their design and interpretation.

Our first experiment used a visual search paradigm that was adapted from the design in Chen and Seidemann (2012). The observer detected Gabor patches superimposed onto orthogonal pedestals at four possible locations. We manipulated attention by varying the number of locations relevant for the perceptual judgment (i.e., varying the relevant set size; Palmer, 1994; Palmer, Ames, & Lindsey, 1993). In the focal cue condition, the relevant set size was 1, and that location was indicated by a precue. In the distributed condition, the relevant set size was 4 (all locations precued), and the observer had to consider stimuli at all locations to make a single judgment of target presence or absence (even if more than one target is present). In such a paradigm, we predicted that increasing the relevant set size will impair accuracy simply because of added noise to the decision stage, even if the quality of each individual sensory representation is unaffected (Chen & Seidemann, 2012; Palmer, 1994). Our technique allowed us to assess divided attention effects both on behavioral accuracy and on stimulus representations in early visual cortex.

Our second experiment used a dual-task paradigm, in which target Gabors were embedded in dynamic noise, and there were only two possible locations rather than four. The task required the observer to make independent judgments of stimuli at each location, rather than combine information about all of them. In the distributed cue condition (i.e., dual-task condition), the observer attended to both locations, and after the stimuli disappeared, she or he was prompted with a postcue to make a judgment about just one of them, disregarding the other. The postcue reduces spatial uncertainty at the decision stage. We compared the distributed cue condition to a focal cue condition (i.e., single-task condition) in which the observer knew in advance which location she or he would have to judge at the trial's end.

In both experiments, we assessed two effects of attention on our behavioral and neuronal measures: (a) the selective attention effect, which is the difference between responses to cued and uncued stimuli in the focal cue condition, and (b) the divided attention effect, which is the difference between responses to focal cued stimuli and the mean response to all stimuli in the distributed cue condition. In both experiments, we found evidence that observers could divide attention across multiple locations. There was no behavioral deficit in the distributed compared with focal cue condition and little to no reduction of response magnitudes in retinotopic visual cortex. These data support the hypothesis that for certain simple tasks and stimuli, there is no cost to dividing attention across multiple spatial locations.

Experiment 1

As described above, our first experiment was designed to estimate both selective and divided attention effects as done by Chen and Seidemann (2012). One alteration we made to their design was based on the work of Shaw (1984). In her visual search task, all stimulus locations were independent of one another in terms of whether each contained a target. As a result, there could be multiple targets in any one display. This differs from the typical search paradigm that restricts the displays to contain only one or zero targets, which means that the locations are not independent of one another. We adopted Shaw's approach because spatial independence allows us to keep the physical displays constant across attention conditions. Thus, an attentional precue that restricts the number of task-relevant locations does not give any information about what will appear in the whole search display. This is especially desirable for our imaging analysis: We can compare fMRI responses to each location across attention conditions that do not differ in visual stimulation.

Methods

Subjects

Six subjects (three men, three women) participated in Experiment 1, ranging in age from 23 to 31 years. All had had normal or corrected-to-normal vision. One of the subjects was author ER. All subjects were compensated at $20/hr. All subjects gave written and informed consent in accord with the human subjects Institutional Review Board at the University of Washington, in adherence to the Declaration of Helsinki.

Stimuli and procedure

Figure 1 shows a schematic of the procedure applied during single trials for both fMRI and behavioral experiments. The subject began by foveating a square on the center of a gray screen (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. There were four possible locations: one in each quadrant of the visual field. Subjects were cued to detect targets at either one location ("focal" condition) or all four locations ("distributed" condition). In the distributed condition, the task was to report whether one or more targets were present at any of the four locations, whereas in the focal condition, the task was to report target presence or absence at just the cued location.
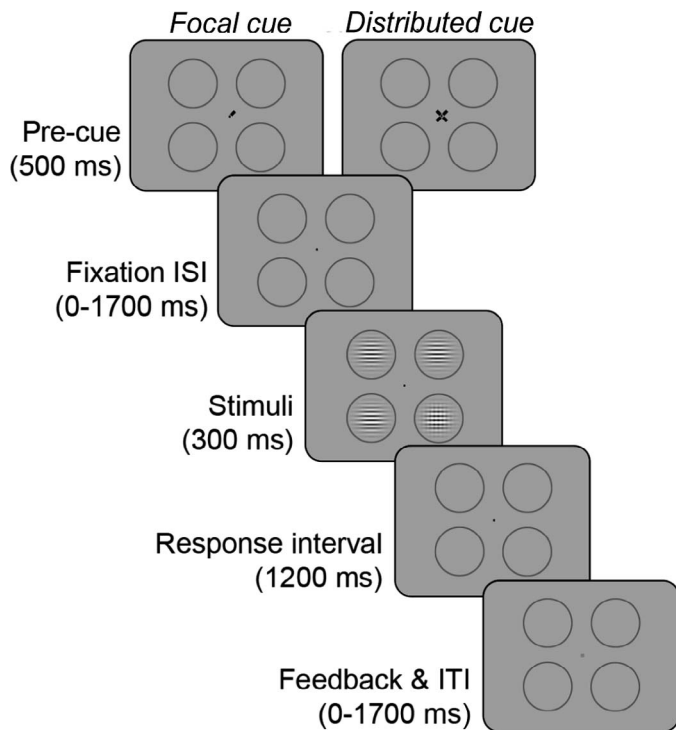
Figure 1. Example trial sequence in Experiment 1. The precue could be directed to one of the four visual quadrants (focal) or all four quadrants (distributed). The size of the cue is exaggerated for purpose of demonstration. In this example, a vertical target Gabor is present in the lower right location.

After a variable stimulus-onset interval (varied between 0 and 1700 ms), four horizontally oriented circular Gabor patches (two cycles per degree, Gaussian standard deviation of 1°, 20% contrast) appeared simultaneously within each quadrant (one per quadrant, centered 5.66° 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% and 1.7%). During the fMRI experiment, the contrast of the target was constant within subjects and across conditions. A target appeared at each location with a probability of 0.2755, independently across trials, locations, and whether it was a focal or distributed condition. This value was chosen so that the probability of a single target appearing at a single location (0.2755) was the same as no target appearing at any of the four locations $(1–0.2755)^4$. When present, targets appeared simultaneously with pedestals, remained on the screen for 300 ms, and then disappeared with the pedestals.

The subject's task was to report their 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 1,500 ms after stimulus onset. Immediately after the response 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 lower two and upper two confidence ratings (*very unlikely* and *unlikely*; *likely* and *very likely*) 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).

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 cue conditions. Stimulus properties such as size, pedestal contrast, and background contrast were matched to those used in the subsequent scanning sessions. For practice only, we reduced the duration of the fixation intervals from 12 s to 3 s to save time.

A second practice session took place with subjects performing the task while lying in the bore of the scanner (no fMRI data collected) to assimilate the subject with the exact conditions to be encountered during the imaging experiment. Also, because of differences in display equipment, the appropriate target contrast levels estimated in the lab often needed to be slightly adjusted for the scanner environment. Around 1 hr per subject was devoted to practice in the scanner.

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 session: After practice, each subject participated in a single fMRI scanning session. 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 × 2.75 × 3.4 mm). Anatomical images were acquired using a standard T1-weighted gradient echo pulse sequence.

We collected 16 functional 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). Scans alternated between focal and distributed cue conditions.

Each experimental scan consisted of six blocks of 12-s fixation intervals followed by 16-s trial intervals. The trial intervals contained four 4-s trials. At the beginning of each trial interval, low-contrast circular outlines appeared around the four stimulus locations (co-centered with stimuli, radius 3°) 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 via the cues that directed attention.

Data analyses

fMRI analyses: We used standard phase-encoding retinotopic mapping procedures to define visual areas V1, V2, V3, and V4 (Engel, Glover, & Wandell, 1997). 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 ($SD = 1°$). We therefore restrict our analyses to V1, which contained four ROIs: one corresponding to each visual field quadrant. All preprocessing (anatomical-functional co-registration, conversion to standardized Talairach space, slice-scan time correction, motion correction, and linear trend removal) was performed using BrainVoyager. We then imported preprocessed fMRI voxel time courses imported into Matlab for analysis with custom software. For each individual voxel in a given ROI (V1), we analyzed the time course of response to each trial interval. That time course was converted to units of percent signal change by normalizing by the mean response over the last three time points of the preceding fixation interval. We then estimated the response to that trial interval by averaging normalized time points 7–16 (in seconds, relative to the start of the first trial). Those values were then averaged across trial intervals, voxels, and scans of identical conditions to produce five summary data points per ROI: one for each of the four selective attention conditions (cue to each of the four quadrants) and one for the divided attention condition. Note that

in this blocked design, it is not possible to estimate the response to individual trials nor to separate trials with and without a target stimulus added to the pedestals. However, the stimulus statistics and target probabilities at each location were independent of the cue condition, and nothing other than the Gabor stimuli was ever presented in the visual field regions for which the ROIs were selective.

To calculate the effect of selective attention, we determined the response to the focal cued stimulus by averaging the four focal cued condition summary data points across ROIs. To calculate the response to an uncued stimulus, we then averaged the summary data points from the ROI representing the visual quadrant diagonally opposite to the cued location. The estimated response to the focal uncued stimulus was subtracted from the response to the focal cued stimulus for each subject, and the effect of selective attention was derived by taking the mean of the differences across subjects.

Similarly, the effect of divided attention was obtained by first calculating the response to stimuli in the distributed condition by averaging the distributed condition summary data points across all four ROIs. The effect of divided attention was then calculated by subtracting the response to the unattended stimulus in the focal cue condition from the response to the distributed cue condition.

To evaluate the statistical significance of pairwise differences between conditions, we conducted standard dependent-measures t tests, as well as nonparametric bootstrapping. For each of 10,000 simulated experiments, we resampled five observers with replacement from our original set of five, and for each observer, we resampled with replacement a new set of BOLD responses from the original set of scans and then averaged over those scans. We then computed the average within-subject difference between conditions for that bootstrap repetition. After 10,000 repetitions, we computed 95% confidence intervals (CIs) on the distribution of bootstrapped mean differences. These CIs were "bias-corrected and accelerated" (Efron, 1987).

Behavioral analyses: We collected behavioral responses during the imaging experiment and assessed them using signal detection analysis (Green & Swets, 1966). The distribution of responses across the four confidence levels (regarding target presence) allowed us to construct receiver-operating characteristic (ROC) curves. We characterized observers' detection accuracy with the area under the ROC curve (A_g, also known as Green's area; Pollack & Hsieh, 1969). A_g is a measure of sensitivity independent of bias, which is especially important in this design, because the correct answer was "target present" more often in distributed cue than focal cue trials. Observers may adopt different decision

criteria in those two conditions, but A_g should capture only differences in sensitivity.

Except where otherwise noted, we restricted the ROC analysis to include only trials that contained only one or zero targets, because performance with multiple targets is affected by the "redundant target effect" (Miller, 1982; Palmer, Verghese, & Pavel, 2000; Shaw, 1982; Verghese & Stone, 1995), whereby additional targets increase the probability to detect any target. We constructed ROC curves in the focal cued and distributed conditions by plotting five pairs of hit and false alarm rates against each other. Each point represents the probability of a hit (responding positively to a target at the cued location[s]) and the probability of a false alarm (responding positively when there was no target at any location) at a particular response level. At the highest level, no trials are represented as target-present responses, yielding hit and false alarm rates of 0 and anchoring the curve at the origin. One level down, only responses of *very likely* are considered target-present responses. One more level down, responses of *very likely* or *likely* are considered target-present responses, yielding somewhat higher hit and false alarm rates, and so on. At the lowest level, all responses are considered "target present," generating a final point that anchors the ROC curve to the upper right corner. The more hits and fewer false alarms, the greater the area under the curve, and the more sensitive the observer is to the difference between target-present and target-absent trials. We computed the area under the curve, A_g, by sequentially connecting each of the five points with a straight line and calculating the geometric area contained below that line.

We also computed ROC curves for the uncued stimulus in trials with a focal cue. For each response level, the uncued hit rate was the proportion of positive responses on trials with no target at the cued location, but one target at an uncued location. The uncued false alarm rate was the proportion of positive responses on trials with no target at any location. We then calculated uncued A_g as the area under the curve formed of pairs of these uncued hit and false alarm rates, as before.

One subject (S3) produced A_g values very near 0.5 (chance detection) during all conditions. Thus, there was no evidence that S3 was attending and responding as directed, and this subject was removed from all other analyses. Single-subject behavioral data are shown in Table 1.

Results

Behavioral performance

Using a visual search task for simple features, we tested the hypothesis that divided attention does not

Subject	Target contrast	Focal cued A_g	Distributed A_g	Focal uncued A_g
S1	1.5%	0.85	0.71	0.56
S2	1.7%	0.75	0.62	0.41
S3	1.3%	0.53	0.48	0.53
S4	1.4%	0.60	0.69	0.45
S5	1.4%	0.64	0.71	0.47
S6	1.5%	0.72	0.65	0.52

Table 1. Single-subject behavioral performance during fMRI. *Notes:* Target contrast indicates the contrast of all vertical Gabors superimposed on 20% contrast Gabors (pedestals). See the Methods section for a description of the ROC analysis and computation of Green's area (A_g).

reduce behavioral accuracy or physiological responses in human V1, relative to focal selective attention. Detection accuracy (area under the ROC curve, A_g) is reported for each subject in Table 1 and plotted in Figure 2A. We assessed two within-subject attentional effects in the data: the selective attention effect and the divided attention effect (plotted in the right panel of Figure 2A).

Selective attention: We assessed the effect of selective attention on target detection in focal cue trials by comparing the A_g values from the focal cued and uncued conditions within subjects. Cued A_g was moderately high ($M = 0.71$, $SEM = 0.04$), but uncued A_g was near chance ($M = 0.48$, $SEM = 0.03$), which indicates that the observers were able to ignore targets at uncued locations such that their presence or absence did not affect responses to the cued target. The difference between cued and uncued A_g was on average 0.23 A_g and reliable across observers ($SEM = 0.04$), dependent-samples $t(4) = 6.29$, $p = 0.003$.

Divided attention: Mean accuracy in the distributed cue condition was 0.68 ($SEM = 0.02$) and not reliably lower than in the focal cued condition. The mean A_g difference was 0.04 and not statistically significant ($SEM = 0.05$), dependent-samples $t(4) = 0.73$, $p = 0.51$. Note that in a search task like this, even models with independent perceptual processing predict divided attention costs on accuracy because of noise at the decision stage, where each additional relevant location introduces a chance for error (Chen & Seidemann, 2012; Palmer, 1994; Palmer et al., 1993). But in this experiment, with relatively few trials per observer in the scanner, the small cost was not detectable.

In that regard, our study did not strictly replicate Chen and Seidemann (2012), who did find a significant reduction in behavioral accuracy in a distributed cue condition. However, our design was not exactly the same as theirs: Their monkeys were required to localize the target by saccading to it, and there could never be more than one target per trial. In
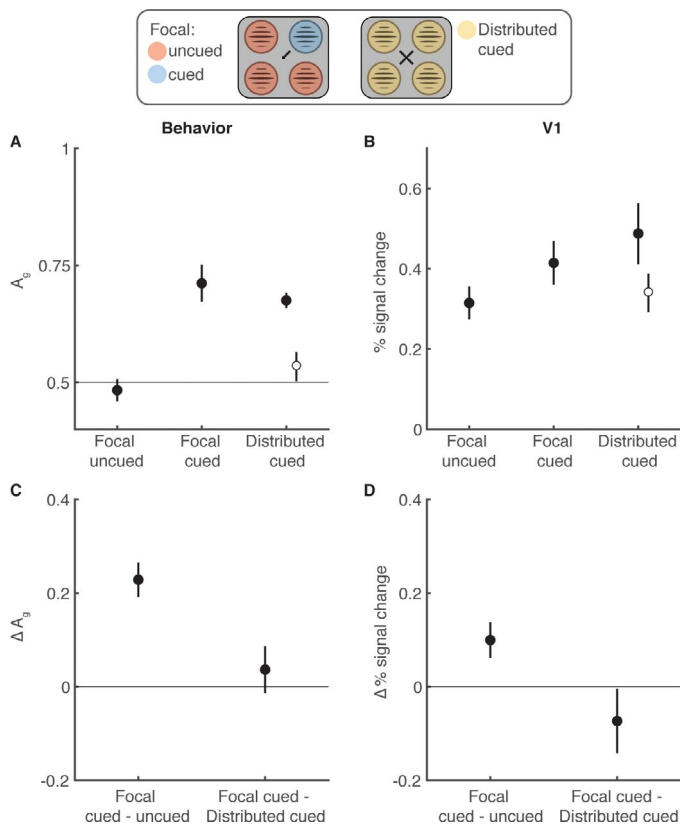
Figure 2. Behavioral (left column) and fMRI (right column) data from Experiment 1. The conditions are illustrated in the legend at the top. "Focal uncued" data are the mean of responses to the three uncued stimuli (for behavior) or the mean response to the stimulus opposite the cued stimulus (for fMRI) in trials with the focal cue; "focal cued" data are the mean response to the single cued stimulus in the same trials; "distributed cued" data are the mean of responses to all four stimuli in distributed cue trials. (A) Behavioral accuracy in units of area under the ROC curve (A_g). (B) Mean BOLD responses in area V1 in each attention condition. (C) Differences in behavioral A_g between two pairs of conditions. (D) Differences in V1 BOLD responses between the same two pairs of conditions. All error bars = ±1 *SEM*. Solid points = data; open points = model predictions for divided attention under the all-or-none switching model (see text).

contrast, our observers merely had to report the presence or absence of any target, and given that all four locations had independent probabilities of target presence, there could be more than one at a time. These differences could contribute to the apparent difference in the divided attention effect on behavioral accuracy.

The above analysis excluded trials with more than one target, to compare focal and distributed cue accuracy levels with appropriately matched trials (as there can only ever be zero or one target at the focal cued location). But within the distributed cue condition, we did find a redundant target effect: With multiple targets, the mean A_g increased to 0.78 relative

to 0.68 from trials with a maximum of one target. The mean difference of 0.10 between those two conditions was reliable (*SEM* = 0.04), $t(4) = 2.48$, $p = 0.04$. However, including all trials (regardless of the number of targets) did not change our conclusion about the difference between focal and distributed cue conditions: In this analysis, mean A_g values were nearly equal (0.71 vs. 0.72, respectively; mean difference = 0.01), $t(4) = 0.3$, $p = 0.77$.

fMRI responses

The mean V1 BOLD responses to blocks of trials (relative to intervening blank fixation intervals) are plotted in Figure 2B. We assessed the same two attentional effects as for the behavioral data (Figure 2A).

Selective attention: In focal cue trials, BOLD responses to focal cued stimuli were higher than to uncued stimuli. The mean within-subject difference in BOLD signal change was 0.10% (*SEM* = 0.04%; bootstrapped 95% CI = [−0.02, 0.19]). Given our prediction, based on prior physiological and neuroimaging work, that responses to attended stimuli should be greater than responses to ignored stimuli, we conducted a one-tailed dependent-samples t test on this selective attention effect, which was significant, $t(4) = 2.62$, $p = 0.029$. This effect was robust regardless of which, or how many, of the uncued ROIs were included in the calculation of the uncued mean.

Divided attention: The primary goal of the experiment was to measure the effect of dividing attention on responses in the primary visual cortex. The effect of divided attention (focal cued − distributed cued) on the BOLD signal was slightly negative ($M = −0.07\%$) and not significantly different from zero (*SEM* = 0.07%, bootstrapped 95% CI = [−0.23, 0.09]), dependent-samples $t(4) = −1.07$, $p = 0.345$. This lack of divided attention effect in V1 is similar to the results of the optical imaging study by Chen and Seidemann (2012), which used similar stimuli and behavioral paradigm. In contrast, previous human fMRI research has shown robust effects of divided attention in early visual cortex, but these studies used relatively complex stimuli and/or change detection tasks (McMains & Somers, 2005; N. Müller et al., 2003; Pestilli et al., 2011).

Modeling an effect of divided attention

The statistical comparisons of the focal- and distributed cue conditions suggest that fMRI responses are just as high and behavioral responses are just as accurate when dividing attention across multiple locations as when attending selectively to a single location. We went further to compare our results to the

predictions of a particular quantitative model of divided attention: the all-or-none switching model. This model assumes that attention can be devoted to only a single location during each 300-ms stimulus presentation, so the observer selects a single random location for full processing on each distributed cue trial. The probability of any single location being attended on a given trial is then 0.25. We then assume that responses (behavioral and neural) to the one attended location should be equivalent to the focal cued responses and responses to the other three stimuli are equivalent to the focal uncued responses. These assumptions allow us to predict behavioral sensitivity for each subject and BOLD responses for each scan in the distributed cue condition. Averaging across locations and trials, the predicted values for divided attention fall one quarter of the way between the corresponding uncued and cued values measured in the focal cue trials.

For the behavioral data, the predicted distributed cue A_g is plotted in Figure 2A (left panel, open symbol). Within subjects, the mean difference between the predicted distributed A_g and the measured distributed A_g was 0.14 ($SEM = 0.03$), dependent-samples $t(4) = 4.25$, $p = 0.013$. We can therefore reject the all-or-none switching model and accept the notion that subjects efficiently selected multiple locations on any given trial in the distributed cue condition.

For the imaging data (Figure 2B), the mean difference between the predicted and measured BOLD signal change in the distributed cue condition was 0.15% and not statistically significant ($SEM = 0.08\%$), dependent-samples $t(4) = 1.78$, $p = 0.149$; bootstrapped 95% CI = [−0.04, 0.32]. Hence, although there was no hint of a divided attention effect in V1, we cannot reject the switching model based on the neuroimaging data alone.

The null-hypothesis testing described above produces an ambiguous result and is unable to tell which model best matches our fMRI data. To reveal more, we took a Bayesian approach of comparing the likelihoods of two models, given the data:

M$_1$: Unlimited-capacity parallel processing: BOLD responses in the distributed cue condition have the same mean as responses to focal cued stimuli.

M$_2$: All-or-none serial switching: BOLD responses in the distributed cue have a mean ¼ of the way between focal cued and uncued responses.

We formalized both models with Gaussian distributions that were assumed to have the same standard deviation: the mean of the standard deviations of the focal cued and uncued responses. (The switching model's standard deviation cannot be estimated independently, because its predicted values are computed via a transformation of focal cued and uncued responses.) We then computed the likelihood of the whole data set D given both models: $p(D \mid M_1)$ and $p(D \mid M_2)$. For each model j, that likelihood is:

$$p(D|M_j) = \prod_{i=1}^{N} p(R_i|M_j)$$

where R_i is the mean BOLD response in the distributed cue condition for subject i and the probability p is computed from the Gaussian probability density function with the mean and standard deviation assigned to model j. We then computed the likelihood ratio Λ for the two models. We also assume a flat prior, that is, $p(M_1) = p(M_2) = 0.5$. According to Bayes Rule, therefore, the likelihood ratio Λ is equivalent to the ratio of posteriors:

$$\Lambda = \frac{p(D|M_1)}{p(D|M_2)} = \frac{p(M_1|D)}{p(M_2|D)}$$

Furthermore, given that both of our models have zero free parameters, the likelihood ratio Λ is equivalent to the Bayes factor (Kass & Raftery, 1995). We found that $\Lambda = 17.8$, favoring Model 1 (no divided attention effect) over Model 2 (switching model).

In summary, both the behavioral and neuroimaging data in Experiment 1 were consistent with independent capacity-free processing of simple features at multiple locations during visual search. Relative to when attention was focused on one stimulus, there was no cost to behavioral accuracy when attention was divided and no reduction in the magnitude of V1 responses. In the next experiment, we sought to generalize our results with a different paradigm and stimuli that might provide greater signal-to-noise ratios in visual cortex.

Experiment 2

The second experiment used a dual-task design rather than visual search (Figure 3). The task was again to report the presence or absence of brief Gabor stimuli, but there were only two possible locations, and there was a postcue at the end of every trial that instructed the observer which single location to judge. A precue instructed the participant either to attend to one side and to ignore the other (focal cue trials) or to attend to both sides (distributed cue trials). At the end of each distributed cue trial, a postcue prompted observers to judge one of the attended locations independently of the other. The focal cue condition could also be labeled the "single-task" condition, whereas the distributed cue condition is the "dual-task" condition, because both stimuli must be analyzed independently. Attentional effects with this paradigm may differ from the search paradigm for at least two reasons: First, only in the search paradigm does
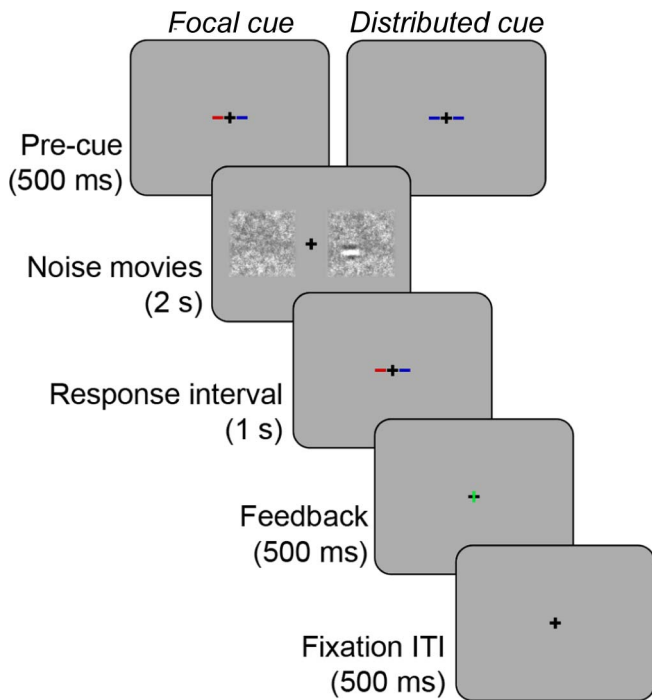
Figure 3. Example trial sequence in Experiment 2. In this example, the blue cues indicate potential target locations. A target Gabor is present in the noise movie on the right.

increasing the number of attended locations risk impairing performance simply by adding noise to the decision, because the observer must combine over multiple noisy representations. The postcue reduces spatial uncertainty to minimize divided attention deficits cause by noise at the decision stage. Second, an observer in the search paradigm might hope to benefit from redundant targets presented simultaneously at multiple locations, whereas in the dual-task paradigm, she or he has the additional challenge of judging each location separately. Our goal in Experiment 2 was to broaden the scope of our findings by using this dual-task paradigm. In addition, the target stimuli were embedded in 2 s of dynamic noise, which we expected would produce stronger cortical responses than the brief Gabor pedestals in Experiment 1.

Methods

Subjects

Six subjects (aged 21–34 years; four men) participated in Experiment 2 (none of whom participated in Experiment 1). All had normal or corrected-to-normal vision. One of the subjects was author AW. All subjects received $30/hr for MRI sessions and $10/hr for behavioral sessions. All subjects gave written and informed consent in accord with the human subjects Institutional Review Board at the University of Washington, in adherence to the Declaration of Helsinki.

Stimuli and procedure

Figure 3 illustrates the display and trial sequence. Observers began each trial by fixating a small ($0.3° \times 0.3°$) black cross at the center of the screen for 0.5 s. Then a precue appeared. It was composed of two horizontal line segments ($0.35°$) on either side of fixation, with their inner endpoints $0.25°$ from the screen center. Each line was blue or red, depending on the attention condition (see below). After 0.5 s, the precue disappeared, and two patches ($6° \times 6°$) of dynamic noise appeared to either side of fixation, centered at $4°$ eccentricity on the horizontal meridian. The noise "movies" played with an effective frame rate of 30 Hz for 2 s and had $1/f$ power spectra in space and time. The movies were generated as follows: Each frame was first populated with independent Gaussian noise at each pixel, with mean 0 and unit variance. The frame was then filtered using a Fourier transform such that the amplitude of each spatial frequency component f_s was proportional to $1/f_s$. Then, the whole movie was similarly filtered in time (via convolution) so that the amplitude of each temporal frequency f_t was proportional to $1/f_t$. The pixel values were then rescaled to have a standard deviation of 0.12 (a relatively low luminance contrast). The local contrast of each frame was attenuated at the edges by a linear ramp down to zero beginning $0.5°$ from the nearest edge.

The observer's task was to detect a Gabor patch embedded within the noise movies. The Gabor was a horizontally oriented sinusoidal grating, with spatial frequency 1 cycle/$°$, windowed by a 2D Gaussian with $SD = 0.5°$ (total width $= 2.5°$). It could appear anywhere within the noise image, as long as its edges were at least $0.5°$ from the edges of the image. The Gabor's contrast was modulated in time by a Gaussian envelope with $SD = 33$ ms. The moment of maximal contrast was chosen from a uniform distribution, excluding the first and last 200 ms of the movie. On each trial, there was a 50% chance that one Gabor was present in the movie on the left and an independent 50% chance that a Gabor was present in the movie on the right.

After the noise movies finished, a postcue appeared, which was composed of the same colored lines as the precue. One line was red and one blue. Each observer was assigned one color for the entire experiment, and after seeing the postcue, she or he reported whether or not a Gabor was present within the preceding noise movie on the side indicated by the line of that color. The observer reported Gabor presence or absence by pressing one of two buttons on a button box held in the hand on the same side as the postcue (i.e., she or he responded with the left hand when asked about the left

side and vice versa). The observer had 1 s in which to respond. At the end of that 1-s response interval, feedback was provided: The vertical arm of the fixation cross turned green if the response was correct, red if the response was incorrect, or blue if neither of the two relevant buttons was pressed within the 1-s interval. The fixation mark remained colored for 0.5 s, after which it returned to black, and 0.5 s later, the next trial began with a precue.

The attention condition was controlled by the precue and was constant within each block of seven trials. In the focal cue trials, the precue was composed of one red and one blue line, exactly matching the postcue. Thus, the observer knew in advance which location she or he would be asked about at the trial's end and could completely ignore the other location. The left stimulus was cued in half of the focal cue blocks, and the right was cued in the remainder. In distributed cue trials, both precue lines were of the observer's assigned color, and the observer had to attend equally to stimuli on both sides, waiting until the postcue to know which location to judge.

In addition, four of the six subjects were presented with blocks of single-stimulus trials, in which noise movies were presented only to the left or only to the right. Those data are not relevant to the main research questions in this article and are not included in the analyses that follow.

Practice sessions: Each observer was first trained in the Gabor detection task for at least two 1-hr sessions outside the scanner, in a psychophysics testing room. Stimuli were generated via an Apple Mac Mini computer and presented on a 35-cm ViewSonic CRT monitor operating at 120 Hz. The display was calibrated to linearize the luminance output. The Gabor contrast was gradually reduced until performance in the focal cue condition stabilized at roughly 80% correct. The contrast from training was usually also appropriate during the MRI sessions, but some adjustment was necessary to stay near the observer's threshold. That adjustment was made during practice trials at the start of each scanning session (when possible), and then the contrast was held constant for all experimental conditions. The average Gabor contrast was 24.1% (range = 21.0%–26.75%).

fMRI scanning sessions: We used the same Phillips 3T scanner as in Experiment 1. Anatomical images were acquired using a standard T1-weighted gradient echo pulse sequence (1-mm resolution). Functional images were acquired using an echo planar sequence, with a 32-channel high-resolution head coil, a repetition time of 2 s, and an echo time of 25 ms. Thirty axial slices (80 × 80 matrix, 240 × 240 × 104-mm field of view, 0.5-mm gap) were collected per volume (voxel size: 3 × 3 × 3 mm). During scanning sessions, the stimuli were generated via an Apple Macbook Pro laptop and back

projected onto a fiberglass screen via an Epson Powerlite 7250 projector. The display was calibrated to linearize the luminance output.

Within each scanning session, each observer completed seven to eight main experimental scans. Each scan lasted 264 s and contained six blocks of seven trials each. There were 12-s breaks between blocks, during which the observer simply fixated centrally. In addition, there were 2 s of blank fixation before the start of the first trial and 11 s of blank fixation after the end of the last trial. For the four observers who had single-stimulus conditions, two of the six blocks in each scan were single stimulus (one left and one right), two blocks were distributed cue, one block was focal cue left, and one block was focal cue right. For the observers without single-stimulus conditions, two blocks were distributed cue, two were focal left, and two were focal right. Block order was randomized within each scan.

In addition, we conducted one to two localizer scans within each session. The same noise movies were displayed as in the main experimental scans, except with no Gabors and the noise contrast (*SD* of pixel values before normalization to the [0, 255] range) was raised to 0.5. During each 264-s localizer scan, one noise patch was presented at a time for 16 s, alternating left and right sides, for a total of eight presentations on each side, with 8 s of blank at the end. The observer's task was to detect brief luminance contrast decrements in either the fixation cross or the noise movie. The time between each contrast-dimming event (each randomly assigned to either fixation or noise movie) was set to 2 s plus a value drawn from an exponential distribution, with mean = 6 s and clipped at 10 s. Each dimming event lasted 250 ms. The observer's task was to press any of the buttons on the response boxes within 1 s after detecting any contrast dimming. The magnitudes of the contrast decrements were adjusted for each participant to keep hit rates ~80% to 90%.

Eye tracking: During training sessions, we used a head-mounted Eyelink 2 eye-tracker (SR Research, Ontario, Canada) to provide feedback about fixation breaks. In all but two scanning sessions, the right eye's gaze position was tracked with an Eyelink 1000 tracker positioned outside the bore of the magnet and calibrated at the start of the session. Because of technical difficulties, the gaze position data were not of high enough quality to be analyzed in 50% of scans. However, the observers always believed that their eyes were being tracked and were reminded to strictly follow instructions to fixate centrally during every trial.

Retinotopy: Each observer participated in an additional retinotopic mapping session, composed of six fMRI scans. In each scan, we presented one of three periodic stimulus types: a contracting ring, a rotating wedge, or alternating vertical/horizontal bow ties. All stimuli

were composed of sections of radial checkerboards counter-phase flickering at 8 Hz. During each 256-s scan, the stimulus made eight "cycles" (rings contracting from 11° to 0.4° radius; wedge rotating clockwise one full circle; bow ties presented vertically then horizontally). Using standard methods (Engel et al., 1997), we analyzed rings and wedge scans to identify the phase of the cycle that each voxel preferred, providing eccentricity and polar angle maps, respectively. A simple general linear model (GLM) analysis on the bow-tie scans, contrasting horizontal and vertical stimuli, provided meridian maps, locating the regions of visual cortex representing the horizontal and vertical meridians. Using these activity patterns, we drew borders between areas V1, V2, V3, V3AB, and V4 on inflated representations of each observer's cortical hemispheres. With these borders, we defined collections of anatomical voxels belonging to each retinotopic region, used to constrain the analysis of the main experimental data (see below).

Data analyses

fMRI analyses: Using BrainVoyager™ software, we preprocessed each functional scan as follows: trilinear slice time correction; motion correction to the first volume of the first scan (trilinear detection and sinc interpolation); phase-encoding distortion correction, based on one volume collected in the opposite direction at each session's beginning; and high-pass temporal filtering (cutoff of two cycles/scan). Each functional scan was co-registered with a high-resolution anatomical scan collected in the same session, which was itself co-registered with the anatomical scan from the retinotopy session.

We defined ROIs with a GLM analysis of the localizer scans, contrasting responses to noise movies on the left and right. The GLM requires a fixed form of the hemodynamic response function, which we set to a three-parameter Gamma function (Boynton, Engel, Glover, & Heeger, 1996). The parameters were adjusted to maximize the average r^2 values in the localizer analysis: phase delay = 3 s, time constant = 1.25 s, pure delay = 2.8 s. For each stimulus (left and right noise patches), we defined ROIs in the contralateral hemisphere within each of four retinotopic areas: V1 through V4. In each area, we selected all the voxels responding to the contralateral stimulus with an r^2 value of at least 0.33 (i.e., the predicted response in the GLM explained at least 33% of the variance of the voxel's time course). Using cutoff r^2 values of 0.25 and 0.5 introduced slightly more noise in the data (either by including noisier voxels or not enough voxels) but did not change any of the conclusions.

We then used a GLM approach to analyze data from each experimental scan in each ROI (converted to percentage signal change averaged across voxels). The GLM included predictors for blocks of each condition (e.g., distributed cue; focal cue left, etc.), as well as a linear trend and DC component. (Note that this blocked design analysis, like in Experiment 1, averages responses over multiple whole trials.) For each scan, we then collapsed across hemispheres to estimate beta weights from each retinotopic area in three conditions: focal cued, in which the cued stimulus was in the ROI's receptive field; focal uncued, in which the *uncued* stimulus was in the receptive field; and distributed cued, which averaged over responses to both stimuli in trials with the distributed cue. For each scan, we also computed differences between pairs of these beta weights (e.g., selective attention effect = focal cued − focal uncued). Beta weights and differences were then averaged across scans, then across observers. We evaluated the statistical significance of pairwise differences with standard repeated-measures *t* tests as well as nonparametric bootstrapping (as in Experiment 1).

Behavioral analyses: Because in this experiment observers reported target presence or absence without a confidence rating, we analyzed accuracy in units of d' rather than A_g. We computed d' with the standard formula: $d' = z(\text{hit rate}) - z(\text{false alarm rate})$, where z is the inverse of the normal cumulative distribution function. Although the observer was never asked to report Gabor presence at the uncued location during focal cue trials, we can estimate an uncued d' level, which should be zero if the observer was able to completely ignore it. The uncued hit rate was the proportion of trials in which a target was present only on the uncued side and the observer reported "present." The uncued false alarm rate was the proportion of trials in which a target was present on neither side and the observer reported "present."

We bootstrapped d' differences between pairs of conditions by simulating 10,000 repetitions of the experiment. In each repetition, we drew with replacement from our set of six observers and for each observer created new hit and false alarm rates by drawing from binomial distributions with means equal to the true hit and false alarm rates and then computed d' and the across-subject mean difference between conditions. A difference was considered significant if the 95% confidence interval of bootstrapped differences did not include 0. We computed bias-corrected and accelerated confidence intervals according to Efron (1987).

Eye-tracking analysis: We were unable to collect any useable gaze position data from two of the six observers. For the remaining four observers, for each trial we analyzed the right eye's gaze position during the time between the onset of the precue and the onset of the postcue. We cut out segments of the gaze position data in which the tracker lost the eye (e.g.,

during blinks), including in the cut 30 ms before and after the missing segment. That resulted in a loss of <1% of data. We then computed the mean horizontal and vertical gaze positions and detected saccades. Saccades were defined as shifts in gaze position (>0.25° and <12°) with two-dimensional velocities that exceeded, for at least 6 ms, an ellipse with horizontal and vertical radii equal to five times the horizontal and vertical median-based standard deviations, respectively (Engbert & Mergenthaler, 2006).

Results

Gaze fixation

For two of the six subjects, we were unable to collect any usable eye data during scanning, although all observers believed their eye movements were being monitored at all times, were encouraged to fixate, and practiced outside the scanner with online feedback about fixation breaks. For the remaining four observers, we computed the mean gaze position and detected saccades during each trial between the precue and postcue. For all observers, the mean difference in horizontal gaze position between focal cue left and focal cue right trials was less than 0.5° visual angle ($M = 0.25°$, $SEM = 0.10°$). On average, saccades occurred on only 3.9% of focal cue trials ($SEM = 2.4\%$) and on 2.5% of distributed cue trials ($SEM = 1.5\%$). Therefore, observers successfully fixated, and the fMRI patterns are unlikely to be driven by eye movements.

Behavioral performance

Figure 4A plots the average detection sensitivity (d') in each attention condition and differences between conditions. In focal cue trials, uncued sensitivity (d') was near chance ($M = -0.09$), whereas d' for the focal cued stimulus was moderately high ($M = 1.74$). The mean difference between focal cued and uncued d' was 1.83 ($SEM = 0.11$), $t(5) = 16.7$, $p < 0.001$; 95% CI of bootstrapped differences = [1.47, 2.10]. This indicates that observers successfully responded to only the focal cued stimulus. Sensitivity in the distributed cue condition was essentially equal to the focal cued condition ($M = 1.74$), and the mean difference of -0.006 was not reliable ($SEM = 0.09$), $t(5) = 0.06$, $p = 0.92$; 95% CI of bootstrapped differences = [-0.32, 0.28]. Thus, there was no cost to dividing attention on behavioral sensitivity.

fMRI responses

In this design, the measured BOLD responses are primarily driven by the dynamic noise patches, rather than the brief and faint targets embedded in them.
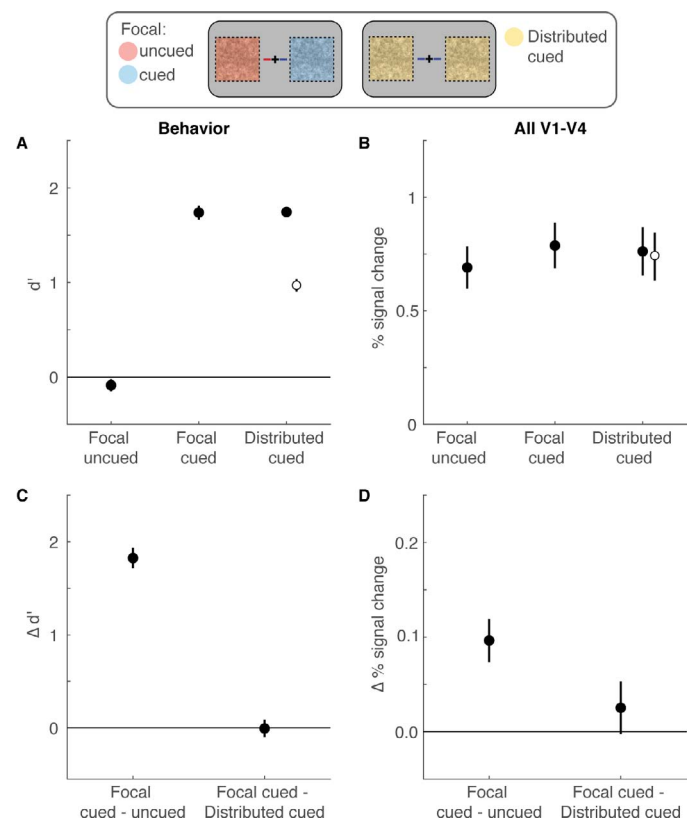

Figure 4. Behavioral (left column) and fMRI (right column) data from Experiment 2. The conditions referred to in the plots are illustrated in the legend at the top. (A) Behavioral accuracy (d') in each cue condition. (B) BOLD responses in a combined ROI that encompasses all of V1–V4. (C) Differences in d' between two pairs of conditions. (D) Differences in BOLD responses between the same pairs of conditions in the combined V1–V4 ROI. Solid points are data; open points are predictions of the switching model for the distributed cue condition. All error bars indicate ± 1 *SEM*.

Similarly, in Experiment 1, the BOLD responses were likely driven by the pedestal Gabors more than the targets superimposed on them. As expected, BOLD responses in Experiment 2 were larger: The mean V1 response to focal cued stimuli was 0.85% signal change, compared with 0.41% in Experiment 1. This is probably because the dynamic noise patches were relatively long in duration and rich in spatial frequency content. But as shown below, the attentional effects were roughly equal in magnitude across the two experiments, likely because visual spatial attention effects measured with fMRI are additive and relatively stimulus independent (e.g., Buracas & Boynton, 2007; Murray, 2008; Pestilli et al., 2011).

We assessed the same two attentional effects on these BOLD responses as before but in separate retinotopic areas V1 through V4 (Figure 5). To maximize sensitivity, we also analyzed a combined ROI contain-
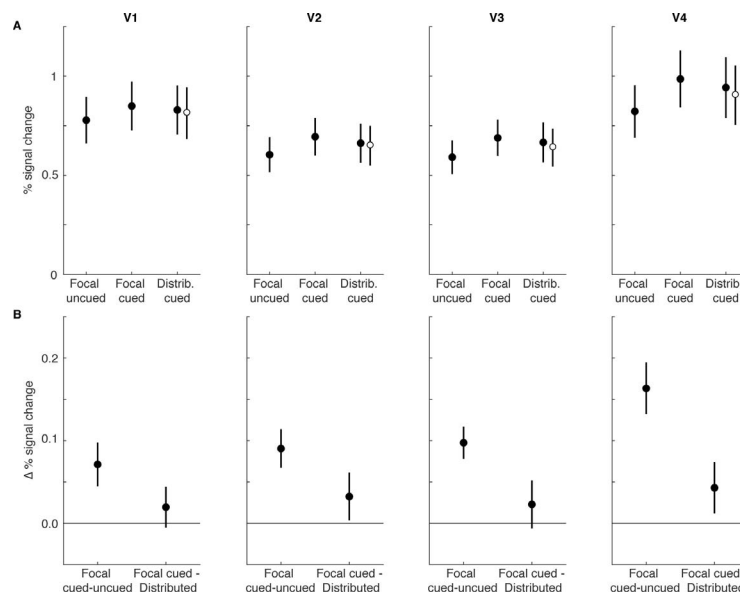
Figure 5. BOLD data from Experiment 2 in individual retinotopic areas. (A) Mean BOLD responses in each cue condition, with a separate panel for each retinotopic area. (B) Mean differences in BOLD responses between two pairs of conditions, in each retinotopic area. Solid points are data; open points are predictions of the switching model for the divided attention condition. All error bars indicate ±1 *SEM*.

ing voxels selected by the localizer scans in all four areas (Figure 4B and 4D).

Selective attention: In the combined ROI (V1 through V4), the mean response amplitude was 0.79% signal change for focal cued and 0.69% for uncued stimuli (mean difference = 0.097; *SEM* = 0.023), $t(5) = 4.28$, $p = 0.004$. The values for each individual retinotopic area are plotted in Figure 5 and listed in Table 2. All areas demonstrated a significant effect of selective attention (focal cued > uncued).

Divided attention: We evaluated the divided attention effect as the difference in BOLD response between attended stimuli in the focal cued condition and attended stimuli in the divided-attention condition. In the combined V1–V4 ROI, the mean response amplitude in the distributed cue condition was 0.76% signal change, not significantly lower than the focal cued response of 0.79 (mean difference = 0.025; *SEM* =

0.03), $t(5) < 1$. The divided attention effect was not reliably greater than 0 in any individual visual area (Figure 5; Table 2). A two-way repeated-measures analysis of variance with factors visual area (V1–V4) and attention condition (focal cued vs. distributed cued) revealed no main effect of attention condition, $F(1) = 1.10$, $p = 0.34$; an effect of visual area, $F(3) = 3.28$, $p = 0.05$; and a nearly significant interaction, $F(3) = 3.14$, $p = 0.06$. The interaction may be driven by the apparently larger divided attention effect in area V4, but neither that interaction nor the effect in V4 alone reached significance (see Table 2).

Modeling an effect of divided attention

As in Experiment 1, we simulated responses in the distributed cue condition under the all-or-none switching model by assuming that half the time

	Focal cued − uncued				Focal cued − distributed cued				
Area	Mean	95% CI	*t*(5)	*p*	Mean	95% CI	*t*(5)	*p*	Λ
V1	0.07	[0.02, 0.15]	2.7	0.022	0.02	[−0.06, 0.09]	0.79	0.46	1.00
V2	0.09	[0.05, 0.16]	3.88	0.006	0.03	[−0.04, 0.10]	1.12	0.31	0.96
V3	0.10	[0.05, 0.15]	4.98	0.002	0.02	[−0.05, 0.09]	0.79	0.47	1.01
V4	0.16	[0.09, 0.23]	5.25	0.003	0.04	[−0.04, 0.13]	1.39	0.22	0.99
V1–V4	0.10	[0.05, 0.16]	4.28	0.004	0.03	[−0.05, 0.09]	0.91	0.4	0.99

Table 2. Summary of fMRI data in Experiment 2, showing statistics for differences between BOLD responses (in units of percentage signal change) for two pairs of conditions. *Notes:* For the focal cued − uncued difference (selective attention effect), *p* values are one tailed. Ninety-five percent confidence intervals (CIs) are based on bootstrapping, corrected according to Efron (1987). The final column lists the likelihood ratios (Λ) for the two competing models of responses in the distributed cue condition.

observers attend only to the left and half the time only to the right. Given that the target stimuli were presented briefly (*SD* of Gaussian envelope = 33 ms) and that they appeared simultaneously when present on both sides, it is unlikely that observers would have been able to process both sides by switching attention from one side to the other *within* one trial. The all-or-none switching model therefore predicts behavioral response rates and BOLD response magnitudes midway between those in the focal cued and uncued conditions (given that there were only two stimulus locations).

For behavioral accuracy, the mean predicted distributed cue d' was 0.96, significantly lower than the measured value of 1.73, $t(5) = 9.78$, $p < 0.001$; 95% CI of bootstrapped differences = [0.46, 1.08]. We therefore rule out the switching model for behavioral sensitivity.

For BOLD responses, the differences between the measured and predicted values (open symbols in Figure 5A) were not statistically significant in any visual area (all *t*-test *p* values ≥ 0.3; all 95% CIs include 0). Therefore, although we found no significant reduction in BOLD response strength for distributed cued compared with focal cued conditions, given the signal-to-noise ratios in our data, we cannot rule out the possibility that there was a divided attention effect as predicted by the switching model. To determine whether we are simply suffering from a lack of power in our data set, we conducted a power analysis by simulating rerunning the experiment, redrawing a variable *N* number of observers, with replacement, from our actual set of six. Even with 48 simulated observers (eight times our sample size), there would be a probability of only 0.30 for rejecting the switching model hypothesis for V1 activity under divided attention (and only 0.55 with 100 observers). The power for rejecting the null hypothesis that there is *no* divided attention effect (focal cued = distributed) hardly better: 0.33 with 48 observers (0.59 with 100). This suggests that we would have gained little by increasing our sample size within the limits of what is feasible.

We also took a Bayesian approach to compute likelihood ratios for two models of BOLD responses in the distributed attention condition, as in Experiment 1:

M_1: Unlimited-capacity parallel processing: BOLD responses in the distributed cue condition have the same mean as responses to focal cued stimuli.
M_2: All-or-none serial switching: BOLD responses in the distributed cue have a mean halfway between focal cued and uncued responses.

These two models were formalized in the same way as in Experiment 1, using a pooled standard deviation for both (the mean of standard deviations of focal cued and uncued responses). Then we computed the likelihood ratio, $\Lambda = p(D \mid M_1)/p(D \mid M_2)$ for the entire data set (see Table 2, right column). Assuming flat priors, Λ is equivalent to the Bayes factor, or the ratio of the posterior probabilities for each model given the data.

The likelihood ratios were equivocal in all areas V1–V4, being near 1. This reflects the fact that mean BOLD responses in the distributed cue attention were roughly midway between the focal cued responses and the switching model predictions. Therefore, there may be some reduction of BOLD responses during divided attention in this task but not as large as would be predicted if only one stimulus were attended at a time. The behavioral data showed no cost of divided attention, however, clearly ruling out the all-or-none switching model and favoring independent parallel processing of the two locations.

Discussion

Summary

Behavioral and neuroimaging data from two experiments with distinct behavioral paradigms supported these three hypotheses: (a) when observers are cued to attend selectively to one peripheral location, behavioral and neuronal sensitivity are higher at that location than others; (b) observers can detect multiple targets defined by simple features in parallel with no cost; (c) correspondingly, early visual cortex processes multiple simple stimuli with no amplitude reduction during divided attention, compared with focal attention. The first two findings have been demonstrated previously, but the third stands in contrast to all previous fMRI studies of divided visual attention, all of which used more complex stimuli and tasks.

To assess these findings, we compared our data to a specific model that assumes it is *not* possible to divide attention across multiple sources without a loss of sensitivity. The attentional switching hypothesis assumes that attention can be devoted to only a single location during any given trial of the distributed cue condition, allowing an all-or-none switching model to predict both behavioral accuracy and BOLD responses in the distributed cue condition, based on the focal cued and uncued conditions. Null-hypothesis tests could not reliably differentiate our BOLD data from the predictions of the all-or-none switching model. Power analyses suggest that the potential differences are so small that impractically large data sets ($N > 50$) would be required to detect them with such statistical tests. A Bayesian analysis of likelihood ratios favored the hypothesis of no divided attention effect in Experiment 1 but equally favored the two models in Experiment 2. In both experiments, however, the behavioral data

clearly rule out the all-or-none switching model, which predicts large costs of divided attention that we did not observe. Altogether, our data lead us to the conclusion that the stimuli in our detection tasks can be processed in parallel at multiple retinal locations with little or no cost.

Our experiments revealed consistent results from two different behavioral paradigms: The first used a search task with brief stimuli appearing at four possible locations and evaluated activity in area V1. The second experiment generalized the findings with a dual-task design and long-duration noise patches at only two locations and with measurements from areas V1–V4. In both experiments, the task was to report the presence or absence of simple Gabor patches with constant features. We believe these common properties of our two tasks are important to understand why our study, unlike most previous, found no effects of divided attention.

Comparison with previous studies of divided spatial attention

Divided attention has been strongly associated with decreased behavioral performance (Braun, 1998; Carrasco, 2011; Harris et al., 2004; Kahneman, 1973). However, a collection of work has shown that processing of multiple sources is unlimited in capacity when the attention-guiding task and relevant stimuli are fairly simple (Bonnel et al., 1992; Busey & Palmer, 2008; Huang & Pashler, 2005; Palmer, 1994; 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 relative to focusing attention on a single-stimulus location. Note that in the search task of Experiment 1, we may have predicted a divided attention cost in accuracy because of statistical uncertainty at the decision stage, as Chen and Seidemann (2012) found. The small accuracy cost we did find was not statistically significant, which could be due to subtle differences in our design or a lack of power. Nonetheless, our imaging results are consistent with those of Chen and Seidemann (2012), who found no effect of divided attention on macaque V1 optical imaging responses.

There is a disparity between our physiological results and those of earlier fMRI studies that found reduced V1 responses during divided attention. McMains and Somers (2005) and N. Müller et al. (2003) used stimuli that are qualitatively complex (color and shape conjunctions; letters) relative to the tuning properties of V1 neurons. In contrast, the oriented Gabor patches used in the current experiment match the tuning properties of early cortical neurons, which may be relevant (see the following section for more discussion).

Moreover, behavioral evidence suggests that detection of color and shape conjunctions is sometimes subject to capacity limitations (e.g., Treisman & Gelade, 1980).

McMains and Somers (2005) used letter stimuli. Although there are examples of unlimited capacity processing of letters (e.g., Eriksen & Spencer, 1969; Pashler & Badgio, 1987), there are also cases in which letters have shown evidence of limited capacity (Kleiss & Lane, 1986; Schneider & Shiffrin, 1977). We propose that the differences in stimulus class between our experiment and those of McMains and Somers (2005) and N. Müller et al. (2003) account for the differences in V1 responses.

Scalf and Beck (2010) reported that divided attention reduces responses in human area V4 in a visual search task with Gabor patches. However, those targets were defined by conjunctions of three features (orientation, color, and spatial frequency) and were presented amidst distractors with partially matching features. The attentional demands of this task differ from ours, in which targets never shared any features with the background or distractors (e.g., Treisman & Gelade, 1980).

Pestilli et al. (2011) reported divided attention effects using a change detection task. Gratings appeared within each visual quadrant, each with a different contrast on a trial-to-trial basis. Across two presentation intervals, one of the gratings (the target) changed contrast. The observer's task was to report which interval contained the higher contrast at the target location. A postcue always indicated target location after stimulus offset. In this case, the rule for detecting a target was also dependent on the pedestal(s). In our simple detection tasks, the target stimulus never changes (vertical Gabor patches in Experiment 1; horizontal Gabor patches in Experiment 2). Change detection tasks produce large set-size effects on behavioral performance (Scott-Brown & 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. In addition, a memory of a first display must be not only maintained and retrieved but also compared with a second display (decision). Both encoding processes (e.g., Irwin, 1992; Rensink, 2002) and decision processes (Hollingworth, 2003; Scott-Brown, Baker, & Orbach, 2000) have been found to affect change detection. Obviously, these processes are not mutually exclusive. We propose that the involvement of memory processes imposed by change detection tasks, which likely played a minimal role in our tasks, contributed to the effects on V1 fMRI responses in Pestilli et al. (2011).

Note that in a subset of trials in the study by Pestilli et al. (2011), the target pedestal contrast was 0%. This

means that the task on those trials was effectively to report which interval contained a grating as opposed to nothing, similar to our yes/no detection tasks. In the plot of those behavioral data, it appears that there may be a marginally significant difference between discrimination thresholds in distributed cue compared with focal cue trials. If that were significant, it would be inconsistent with our finding of no divided attention effect on accuracy in our yes/no grating detection tasks. The model fits to Pestilli et al.'s fMRI data predict a difference between focal- and distributed cue activity at zero pedestal contrast, which would also differ from our findings. We can speculate that other differences in stimulus and task account for these possible differences in results (specifically, Pestilli et al.'s use of demanding change detection task with different stimuli at four locations and unpredictable contrast levels).

In summary, the effects of divided spatial attention on both behavior and cortical responses are dependent on the nature of the stimuli and task. Divided attention impairs performance and reduces cortical responses when the stimuli are relatively complex, when variable features or feature conjunctions define the targets, or when the task requires fine discriminations or places demands on memory. There are no such divided attention effects when the target stimuli are simple and constant and the task is as simple as reporting the presence or absence of an item that differs from its background in a predictable way, as in the two experiments presented here. Note that there may also be an important distinction between endogenous (voluntary, sustained) spatial attention, which we studied here, and exogenous (stimulus-driven, transient) spatial attention. Unlike with divided endogenous attention, observers can perform difficult discrimination or identification tasks with no cost when multiple locations are exogenously cued at the same time (Bay & Wyble, 2014; White, Lunau, & Carrasco, 2014).

Models for behavioral and neural effects of divided attention

Our results relate to, but cannot resolve, two questions that have been long debated in the study of visual attention (Eckstein, Peterson, Pham, & Droll, 2009). First, does attention affect stimulus representations directly, or does it affect decision processes? On one hand, theories of "limited resources" in perceptual processing argue that attended stimuli are encoded with greater fidelity or sensitivity than unattended stimuli (e.g., Carrasco, 2011; Desimone & Duncan, 1995; Kahneman, 1973; Posner, 1980). On the other hand, statistical decision theories argue that attention does not necessarily affect initial stimulus encoding but gives attended stimuli more weight in later decision stages, in which noise and uncertainty also limit behavioral accuracy (Eckstein et al., 2009; Palmer, 1994; Palmer et al., 1993; Shaw, 1982; Sperling & Dosher, 1986).

The second question is, How can we link attentional effects on neuronal measures to attentional effects on behavioral measures? The simplest linking hypothesis for behavioral and fMRI data like ours is that an increase in the mean response in the visual cortex reflects an increase in the signal-to-noise ratio of the relevant variable upon which the perceptual decision is based (Boynton, Demb, Glover, & Heeger, 1999; Buracas, Fine, & Boynton, 2005; Ress et al., 2000; Shadlen & Newsome, 1998). This hypothesis is supported by the fact that our behavioral results mirror our neuroimaging results: Responses to focally attended stimuli are roughly equal to responses during divided attention, and responses to ignored stimuli are lower.

If we accept this simple linking hypothesis, we would then have an answer to the first question: The effect of *selective* attention in our task (difference in responses to focally attended and ignored stimuli) is not a sign of limited resources in perceptual processing, because all the stimuli *can* be perceptually encoded simultaneously with no cost. Indeed, several previous studies have provided explanations for attention effects in visual cortex that do not rely on the concept of limited resources. Chen and Seidemann (2012), who reported V1 optical imaging results that mirror our fMRI results, found a significant selective attention effect that began before stimulus onset and did not reflect a modulation of stimulus encoding strength. The authors suggested that effect was instead a form of "spatial gating" that biases competition at later processing stages in favor of attended stimuli. Similarly, Pestilli et al. (2011) concluded that the best explanation for their observed behavioral advantage in the focused attention condition was enhanced "selection efficiency" of the relevant stimulus due to a baseline shift in its response. In other words, precueing the target location improved performance primarily because it allowed for better exclusion of irrelevant signals from the decision process (or working memory, as the authors acknowledge), rather than increased precision of the target's representation itself. A related electroencephalogram study found that during a task that required classifying the orientations of simple stimuli at one or two locations, dividing attention had little effect on initial stimulus encoding but had large detrimental effects at later stages corresponding to the integration of new sensory evidence into decision variables (Wyart, Myers, & Summerfield, 2015).

Altogether, these results paint a more complex picture of how focused and divided spatial attention affect behavioral and neuronal responses. In fact, the

studies by Chen and Seidemann (2012) and Pestilli et al. (2011) cast some doubt on the simple linking hypothesis that we provisionally accepted two paragraphs ago. They question the assumption that an effect of spatial attention on mean neuronal responses in a particular region of visual cortex implies a change in the quality of the sensory representation at that stage. The responses to (all) attended stimuli may be greater than responses to ignored stimuli by an additive and stimulus-independent factor (see also Buracas & Boynton, 2007; Murray, 2008; Pestilli et al., 2011), which functions to give more weight to relevant stimuli in later stages of evidence accumulation and decision making.

Our results are consistent with that broader conclusion but cannot on their own distinguish between different mechanisms of spatial attention nor possible linking hypotheses between the BOLD response and behavior. See Eckstein et al. (2009) for a detailed review of the challenges these questions pose. We do, however, show for the first time with human neuroimaging that observers are able to divide spatial attention without dampening either behavioral accuracy or BOLD responses in visual cortex. These results cast doubt on the strong view that spatial attention functions as a single "spotlight" that devotes limited processing resources to relevant stimuli. Rather, our results support a hypothesis of unlimited capacity parallel processing. But as we reviewed in the previous section, the mechanism of attention appears to depend strongly on the particular stimuli and task demands.

We further propose that observers can successfully divide attention without cost only if there is an independence of neural processing across regions of visual cortex tuned to the relevant areas of visual space. The degree to which those processes are independent could vary with the distance between attended locations. We designed our stimuli to be widely separated to avoid issues such as crowding and lateral masking. It is possible that divided attention effects depend further on whether the attended locations are in separate hemifields. An across-hemifield advantage for divided attention has been reported for behavioral performance and neuronal responses (Alvarez, Gill, & Cavanagh, 2012; Awh & Pashler, 2000; Scalf & Beck, 2010; Walter, Keitel, & Müller, 2015). In our second experiment, the relevant locations were always in opposite hemifields, which might partially account for the lack of divided attention effect. In the first experiment, however, there were two relevant locations per hemifield, and attending to all of them caused no reduction in behavioral accuracy or BOLD response.

Moreover, the independence we found during divided attention in V1 is plausibly restricted to relatively simple stimuli such as oriented Gabors and gratings, which characterize the spatial response properties of V1 neurons (Heeger, 1992; Movshon,

Thompson, & Tolhurst, 1978). V1 neuronal 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 specific visual tasks (Beauchamp, Cox, & DeYoe, 1997; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990, 1991; Runeson, Boynton, & Murray, 2013). Our second experiment generalized the basic findings to areas V2, V3, and V4. Selective attention effects (focal cued vs. uncued) increased across the cortical hierarchy, but in no area was the divided attention effect (focal cued vs. distributed) significantly greater than zero.

Conclusion

Using two detection tasks with targets defined by simple visual features, we found evidence that fMRI responses in retinotopic visual cortex are not affected by the division of spatial attention. This is in contrast to previous fMRI studies showing signal reductions during divided compared with focused attention. We attribute our finding to independent processing across space by neurons in early visual cortex tuned to the features defining our stimuli. The use of simple (but perceptually challenging) visual tasks minimized the involvement of memory or decision processes, which might play a role in tasks that yield large divided attention effects. In short, our results are consistent with unlimited capacity processing of simple features in visual cortex.

Keywords: divided attention, fMRI, functional imaging, primary visual cortex, spatial attention

* ALW and ER contributed equally to this article.
Commercial relationships: none.
Corresponding author: Alex L. White.
Email: alexlw@uw.edu.

Address: University of Washington, Department of Psychology, Seattle, WA, USA.

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