Effects of Divided Attention for Space and Features

James Kit Moreland

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Reading Committee:

Geoffrey M Boynton, Chair
John Palmer
Andrea Stocco
Wyeth Bair

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University of Washington

Abstract

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Chair of Supervisory Committee:
Professor Geoffrey M. Boynton
Department of Psychology

To cope with the multitude of stimuli in the world, our visual system selectively attends to the pertinent locations or features in our environment, and while not all available information is relevant, it is common at a given moment for there to be more than a single element of interest. What are the behavioral and neural consequences in these cases of divided attention? The experiments described in this dissertation combine careful progressions of psychophysical tasks and fMRI to examine three broad questions (1) Is there always a cost to performance in divided attention tasks? (2) What are the cognitive processes that are limited under conditions of divided attention? (3) How does dividing attention across features at different spatial locations affect neural responses in visual cortex as measured by fMRI?

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Dedication

To my family, I am sorry that my PhD took me so far from you all. I hope that you are proud of what I have achieved with this choice. There are so many points in my life that accumulated to allow me to achieve this work, which was only possible because of your support and inspiration.

Rosemary, you have been an outstanding partner throughout this entire experience. Your patience and unrelenting support for me is astounding.

Chapter 1. Introduction

An extraordinary amount of visual information is available to the human perceptual system at any given moment. In order to extract meaning from the information, the system attempts to select the most relevant parts. For example, when driving, not only do we physically move our eyes to look at relevant objects such as traffic lights, we also covertly shift our attention to identify potential hazards such as pedestrians stepping out into the road. Directing attention in this way acts as a selection of goal-relevant information. In addition to selecting information based on location, the visual system can also enhance relevant features. It might be pertinent when driving to be more sensitive to green while at a stop light.

Despite these flexible selection processes, behavioral performance can still be impaired when there are multiple stimuli relevant to our goals. Differences in performance that depend on the number of relevant stimuli are what we refer to as effects of divided attention. The internal mechanisms that produce these effects are described in terms of capacity limits. Some visual tasks, such as reading, display extreme effects of divided attention and suggest internal mechanisms that are capacity limited, while others do not show evidence of limits.

This dissertation begins with an investigation of the effects of divided attention across spatial locations in a certain type of visual task known as change detection. This particular task has great utility in the study of divided attention because it engages several stages of visual processing (Chapter 2). Chapter 3 goes beyond spatial effects to measure the effects of divided feature-based attention on responses in visual areas V1, V2, V3, V4, and hMT+.

1.1 Divided Spatial Attention in Behavior

A typical method for examining capacity limits in spatial attention has been through the manipulation of relevant set-size where multiple stimuli are present, but only a subset is relevant in a given trial. Keeping the physical stimulus identical while varying the number of relevant stimuli ensures that the capacity of attention is being measured rather than other sensory limits such as crowding (Rosenholtz, 2011). Bonnel, Stein, & Bertucci (1992) displayed two continuously illuminated LEDs and asked observers to detect brief luminance decrement events. Events occurred with an independent 50% chance at either location. Relevant set-size was manipulated using pre-cues occurring prior to the trial initiation. Observers were either cued to one location, indicating that at the end of the trial they would be asked about that location, or they were cued to both locations, indicating that at the end of the trial they could be asked about either side. The question for this study was whether detection performance was the same in these two conditions, or whether performance was limited when two locations were relevant. Any differences between the two conditions would be described as an effect of divided attention. For this simple detection task, they found that performance was equal, suggesting a no capacity limit on dividing attention.

Many studies also exist exploring capacity limits using another type of task known as change detection, which sits in contrast to this simple detection task. In this case, the task involves presenting a set of stimuli in a first interval, then following a delay, a second set is shown and the observer must detect whether one or more of the items changed between the displays. Change detection and its variants have been used to study capacity limits at several stages of processing. For successful task completion, the stimuli must have a sensory representation, which is then encoded and stored in memory before being retrieved and compared following the second stimulus interval. Each of these stages has been implicated in limits of dividing attention. Primarily, monkey physiology work has alluded to sensory limits when effects of divided attention have been observed in single neurons in early visual areas (Cohen & Maunsell, 2010; Martinez-Trujillo & Treue, 2002; Mayo & Maunsell, 2016; Williford & Maunsell, 2006). Human psychophysics more frequently uses change detection in visual memory research (Hollingworth, 2006; Luck & Vogel, 1997; Oberauer & Lin, 2016) or at the comparison/decision processing stage (Mitroff, Simons, & Levin, 2004; Scott-Brown & Orbach, 1998).

Change detection is a complex task, involving many processing stages, any of which could be a source of a limit in dividing attention. The experiments of Chapter 2 systematically work through the processing stages to narrow in on likely candidates for the effects of attention seen in psychophysical change detection tasks.

1.2 Divided Feature-Based Attention in Visual Cortex

The second part of this dissertation moves on from the effects of dividing attention across more than one spatial location to the question of how feature-based attention operates when there is more than one relevant feature value (e.g. red and green). Multiple relevant feature values, such as red and green, is different from multiple relevant feature dimensions, such as red horizontal, which is sometimes referred to as conjunctions in visual search. The work in this dissertation refers only to the former type of feature-based divided attention.

Evidence of feature-based attention has been observed in behavioral performance in cases where there is only one relevant feature value. In visual search for example, the time to detect a conjunction target depends on the number of items that share a relevant feature, but not the total number of stimuli on the display (Moore & Egeth, 1998). A range of methodologies have demonstrated enhanced responses across the visual field for the relevant feature value (single-unit monkey physiology: e.g. Haenny, Maunsell, & Schiller (1988), Martinez-Trujillo & Treue (2002, 2004); functional magnetic resonance imaging (fMRI): e.g. Saenz, Buracas, & Boynton (2002), Serences & Boynton (2007b); encephalography (EEG): e.g. Painter, Dux, Travis, & Mattingley (2014)). These results suggest that the visual system can effectively select stimuli on the basis of a feature.

What happens when more than one feature value is relevant? There are several possibilities for how the visual system could proceed. At one extreme, it might be that only a single feature can be enhanced relative to irrelevant features at a given moment. At the other extreme, each relevant feature could be equally enhanced across the visual field, with either unlimited capacity (i.e. equal to single feature enhancement), or with some parallel capacity limit (i.e. equal but reduced feature enhancement for each relevant feature). A common approach to studying this question has been to have two feature values present at one or two locations and ask the observer to attend to one feature value at each location (Andersen, Hillyard, & Muller, 2013; Lo, Howard, & Holcombe, 2012; Saenz et al., 2002; Saenz, Buracas, & Boynton, 2003; Serences & Boynton, 2007a). When the same feature value is relevant in two locations, psychophysical judgements on those stimuli are facilitated relative to when a different feature value is relevant at each location (Andersen et al., 2013; Saenz et al., 2003). These behavioral results suggest that it is not possible to enhance two features independently at each location and supports a hypothesis that feature-specific activity cannot be spatially constrained. A second experiment by Saenz et al. (2003) suggests that the dependence relates to the presence of the conflicting feature at the same location. When only one feature value was present at each location there was no difference in performance for same versus different features (see also Experiment 2 of Lo et al., 2012). This suggests that there is not only a feature-specific enhancement across the visual field but also some interference from irrelevant stimuli that share another target's feature value.

These divided attention effects have also been observed in the brain using EEG. Steady-state visually evoked potentials (SSVEP) measured the responses to features at different locations and found enhanced activity for the when the same feature value was relevant at two locations relative to when conflicting feature values were relevant (Andersen et al., 2013; Andersen, Muller, & Hillyard, 2015; Forschack, Andersen, & Muller, 2017). This effect was greatly reduced, or eliminated, when the irrelevant features did not share feature values with relevant stimuli. These results suggest that there is feature-specific enhancement across the visual field but reduced responses to irrelevant features are specific to distractors and targets sharing feature values.

To date, there has been no investigation of these effects using fMRI. The challenge is that engaging feature-based attention, and not the effects of spatial attention, requires that multiple feature values occupy the same spatial location (e.g. overlapping colored dots, or motion fields). In the experiment reported in Chapter 3, we measure the response to multiple feature values at the same spatial location by applying a more recently developed technique, which allows us to quantify the magnitude of the attentional effect on both relevant and irrelevant feature values that occupy the same spatial location. Our results show that the effects of divided attention observed in behavior are matched by responses in areas V3 and hMT+ but not by earlier areas.

Chapter 2. Evidence that divided attention effects in change detection are due to retrieval and/or comparison

James C. Moreland, John Palmer & Geoffrey M. Boynton
University of Washington

2.1 Abstract

The change detection paradigm is a common method for investigating limits in dividing attention. Variants of this paradigm have implicated limits in the full range of cognitive processes including perception, memory encoding, memory storage, memory retrieval and decision. In the present study, observers had to detect a change in the orientation of two Gabor stimuli. We were able to determine the source of the limits of change detection by varying when observers were cued that only one of the two stimuli was relevant. Large effects of divided attention were found both when no cue was provided to the relevant stimulus and also when a cue was provided after the second display. However, little or no divided attention effects were found when a cue was provided between display intervals, or when only the relevant stimulus was presented in the second display. Our results are inconsistent with limits in perception, memory encoding and storage. Instead, in this simple change detection task divided attention effects are due to limitations in memory retrieval, and/or comparison processes.

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2.2 Introduction

Effects of attention have been measured collectively at perceptual, memory and judgement/decision stages in a paradigm commonly known as change detection. The typical change detection task consists of presenting two displays of multiple stimuli and asking the observer to judge whether there has been a change between the displays in one or more of the stimuli. Usually, the displays are shown sequentially with a brief separation to prevent transients from signaling the change. For success in this task, the observer must process the sensory input from the first display, encode and store the stimuli in memory, process the second display, retrieve and compare the stimuli representations and make a decision on the basis of this comparison. When displays for change detection contain multiple relevant stimuli, the observer must do all of the processes for multiple stimuli. Any decline in performance for multiple items compared to a single item is a candidate for an effect of dividing attention at some stage of processing. Various implementations of this task have associated limits in change detection performance to the processes within perception (e.g. Pestilli, Viera, & Carrasco, 2007), memory (e.g. Awh, Barton, & Vogel, 2007; Luck & Vogel, 1997; Rouder et al., 2008; Wilken & Ma, 2004; Zhang & Luck, 2008) and decision (e.g. Scott-Brown & Orbach, 1998).

A common method to investigate the capacity limits for divided attention with change detection is to manipulate the number of items in the display, or *set size* (e.g. Griffin & Nobre, 2003; Keshvari, van den Berg, & Ma, 2013; Scott-Brown & Orbach, 1998; Woodman, Vogel, & Luck, 2012). As an example, Keshvari, van den Berg, & Ma (2013) presented observers with an array of oriented lines and, following a short blank, presented a second array of oriented lines. On each trial, there was a 50% chance that one line changed in orientation from the first to the second stimulus display, and observers reported whether or not a change had occurred. To evaluate models of change detection the authors varied the set-size, to manipulate dividing attention. They found that performance declined as set-size increased and the results were interpreted in terms of limits in memory storage. However, while increasing set size undoubtedly increases the load for memory storage, increasing set size also increases the load for other processes including perception (due to crowding, for example), memory encoding and retrieval.

In the present study we always presented a set size of just two stimuli to minimize the effects of perceptual crowding and memory load. Instead of varying set size, we investigated the source of the limits of change detection using cues to vary the number of relevant stimuli. We had observers detect changes in the orientation of a Gabor in noise for either one or two stimuli over two display intervals. Observers were pre-cued to attend either to one stimulus, or to both stimuli. We define difference in performance between the cue-one and cue-two conditions as the *pre-cue effect* and interpret it as an effect of divided attention.

2.2.1 Alternative Theories of Change Detection

There are many theories that posit a limited capacity in perception for divided attention tasks. At one extreme are theories suggesting a bottleneck that allows only one stimulus to be identified at a time (Broadbent, 1958), while other theories are less severe suggesting a limited resource that is divided among relevant items (e.g. Kahneman, 1973). These theories predict that performance in divided attention tasks is impaired because the stimuli are in competition for the limited processing resources in perceptual stages.

Despite these potential limits in perception, change detection is most widely used to test hypotheses about memory. The first display provides a study stimulus to be encoded, stored and later retrieved. The second display provides the test stimulus to which the study stimulus must be compared. Change detection in memory research primarily differs from the use for perception in the types of stimuli used. Rather than using perceptually challenging stimuli such as low contrast Gabors, or small luminance changes, memory research typically uses easily discriminable stimuli such as high contrast bars, colored patches or nameable objects (Luck & Vogel, 1997; Wilken & Ma, 2004). There are many possibilities for limits at each stage of memory. For encoding, stimuli might be moved into memory serially (e.g. Becker, Miller, & Liu, 2013) or in parallel with or without capacity limits (Rideaux, Apthorp, & Edwards, 2015; Rideaux & Edwards, 2016). Storage limits might be in terms of the number of items (e.g. Luck & Vogel, 1997) or of the quality of the representations (e.g. Keshvari et al., 2013). For retrieval, theories propose serial (McElree & Dosher, 1993) or parallel (McElree & Dosher, 1989) access, or an effect of interference during retrieval that depends on the number of relevant stimuli (Oberauer & Lin, 2016). Each of these broad hypotheses - encoding, storage and retrieval - predicts an effect of divided attention in the change detection task.

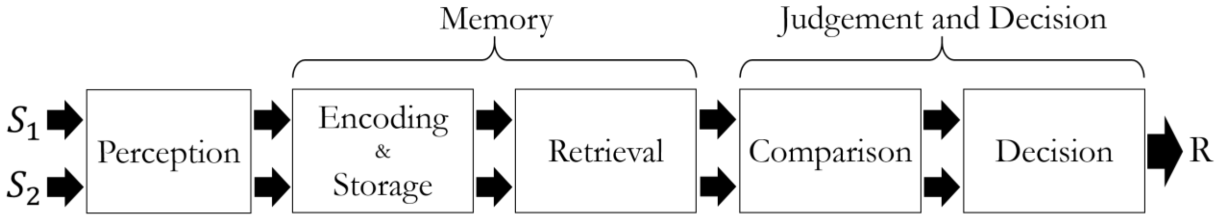


Figure 2-1. Schematic of the stages of processing for the change detection task. Each stage is associated with one or more potentially limiting process and hypothesis to be tested.

Following memory, the final stages of processing in change detection that we will consider are judgement and decision. At the point of decision, observers already have relevant information in memory and need to compare this information in order to make a judgement and response. We will describe limits on the decision processes in two ways. First, as ‘decision noise’ which describes a process as being limited by the variability associated with each stimulus representation (Palmer, Verghese, & Pavel, 2000; Sperling & Dosher, 1986; Swets, Tanner, & Birdsall, 1961). Second, as a limit in the comparison process between the two displays (Angelone, Levin, & Simons, 2003; Farell, 1985;

Fernandez-Duque & Thornton, 2000; Hyun, Woodman, Vogel, Hollingworth, & Luck, 2009; Mitroff et al., 2004; Simons, Chabris, Schnur, & Levin, 2002).

Figure 2-1 shows a schematic of the processing stages and associated hypotheses for the task of change detection. It shows two stimuli moving through each stage. Distinguishing between the hypotheses of limits at each processing stage can be done by the use of cueing. First, a cue before or during the first array (pre-cue) can affect all stages of processing. By allocating attention to the relevant location, performance is improved by prioritizing the quality of the encoded representation (Griffin & Nobre, 2003; Landman, Spekreijse, & Lamme, 2003; Pestilli, Carrasco, Heeger, & Gardner, 2011; Scott-Brown & Orbach, 1998). This prioritization can be imagined in Figure 1 as if only one set of arrows passed through each processing stage - the other stimulus does not require processing. Second, a cue between the two arrays (retention-interval cue; other authors refer to this as a retro-cue) can affect only retrieval, comparison and decision processes because the original encoding opportunity has ended (Beck & van Lamsweerde, 2011; Griffin & Nobre, 2003; Hollingworth & Maxcey-Richard, 2013; Landman et al., 2003; Makovski, Sussman, & Jiang, 2008). In our schematic, this retention-interval cue appears between the encoding and storage stage and the retrieval stage, and only one set of arrows remains past this point. A third type of cue that follows the second stimulus display, the post-cue, does not influence memory stages, but can affect decision processes (Hawkins et al., 1990). This final cue allows one to independently measure the two previous stages without an effect of decision.

2.2.2 Overview of Experiments

In our first experiment, a basic form of change detection was used in which two stimuli were presented in the first display, followed by a blank, then a second stimulus display. The observer's task was to report whether either stimulus changed from the first to the second display. The decision in this task has a many-to-one mapping because a change at either location maps to the same response. This means that any noise in the stimulus representations is compounded across sides and may obfuscate effects occurring in earlier processing stages. To remove this complication, in the second experiment, we introduce a post-cue and independence across sides to make the stimulus response mapping one-to-one. This tests for a contribution from the decision process to the pre-cue effects.

In the third and fourth experiments, we modify the procedure to test the contribution of limits on memory retrieval and comparison. If a process prior to retrieval limits performance, we expect the pre-cue effect with the modified procedure to remain the same as in the first two experiments because nothing about the displays or stimuli have changed up to this point. If, however, change detection is limited by retrieval or comparison we expect the pre-cue effect to be reduced, or in the extreme, eliminated. In summary, these experiments allow one to identify the locus of divided attention effects in change detection.

2.3 General Methods

2.3.1 Observers

Twelve observers participated in each of Experiments 1-4. Of 19 unique observers (3 males, age 18 - 35), five participated in all four experiments, five participated in three, four participated in two and five participated in one (for full details of which experiments each observer participated see Appendix). Order of experiment participation varied for each observer.

All observers had normal or correct-to-normal vision. One of the observers was author JM. All observers (except JM) were compensated $20/hour. All observers gave written and informed consent in accord with the human observers Institutional Review Board at the University of Washington, in adherence with the Declaration of Helsinki.

To determine the minimum number of observers needed to detect an effect we conducted an a priori power analysis based on pilot data from a previous Gabor detection experiment. In the previous experiment, observers (N = 5) each completed 1920 trials (~ 5 hours with a maximum of 1 hour per session) in a simple Gabor detection experiment with stimuli sharing the same parameters as the present experiments (see 'noise movies' and 'gabors' sections below). We observed an effect size of 4.2% ± 1.1%. To ensure that we could detect a smaller effect size of 2% (SD 1.5%; $d_z = 1.33$) 80% of the time using a paired sample t-test we found we required a minimum of 7 observers. For good measure, we chose to use 12 observers in each experiment.

2.3.2 Stimuli and Procedure

In all four experiments, the basic task was to detect whether the orientation of a Gabor in noise changed from a first to a second display. Figure 2-2 shows a schematic of the procedure for single trials for each of the conditions of Experiment 1. Trials were blocked by condition: cue-one (left and right), and cue-both. For all trial types, observers began by foveating a fixation cross at the center of a gray screen (500 ms; 50% of max luminance). This was followed by a pre-cue consisting of two lines on either side of the fixation cross (1° eccentricity; 500 ms). In the cue-one condition, the lines were different colors (red and blue), in the cue-both condition the lines were the same color. Each subject was allocated a cue color that indicated the relevant side (colors were counterbalanced across observers). An earlier version of the experiments did not have a pre-cue in the cue-both condition. However, there was no difference in the results for observers who ran under these conditions so data was collapsed for analysis. Following the pre-cue, a display containing two patches (6° x 6°) of a Gabor added to dynamic noise appeared on either side of fixation, centered at 4° eccentricity on the horizontal meridian. After the first display (1000 ms) there was an inter-display period with only the fixation cross (1000 ms) followed by a second display of a Gabor in noise (1000 ms). After a brief delay with the fixation cross alone (250 ms) a post-cue appeared until the subject responded whether or not the orientation of either cued Gabor changed from the first to the second display interval. For Experiment 1, the post-cue was identical to the pre-cue. Only one response was required. Responses were given on a rating scale (likely-no, guess-no, guess-yes, likely-yes) so that an ROC curve could be determined. Auditory feedback was provided for incorrect responses (180Hz).

Each block consisted of 24 trials from one of the three conditions: cue-both, cue-left and cue-right. A single experimental session included four cue-both blocks, two cue-left blocks and two cue-right blocks. Each observer performed practice sessions in which the Gabor contrast was lowered gradually until performance was stable at ~80% in the cue-one conditions. Observers then completed 10 sessions at this near threshold contrast resulting in 1920 trials overall per subject. Each session took 20-25 minutes, and typically two sessions were run back-to-back within an hour. We also collected four sessions with high contrast Gabors (80% contrast) from each observer to assess performance with highly visible stimuli. Inadvertently, two subjects in Experiment 1 did not complete 1 or 2 low contrast sessions, and two subjects in Experiment 2 did not complete 2 high contrast sessions.

NOISE MOVIES: The "movies" had 1/f noise in space and time and played for 1000 ms with an effective framerate of 30 Hz. The movies were generated as follows: Each frame was first populated with independent Gaussian noise at each pixel, with zero mean and unit variance. The frame was then filtered using a 2D 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 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.

GABORS: The Gabor patches had spatial frequency of 1 cycle/° and were windowed by a 2D Gaussian with a standard deviation of 0.5° and truncated to a total width of 2°. The Gabor could appear anywhere within the noise image, as long as the edges of the truncated width were at least 0.5° from the edges of the noise. The Gabor's contrast was modulated in time by a Gaussian envelope (standard deviation 50 ms). The time of maximal contrast was chosen from a uniform distribution, excluding the first and last 200 ms of the movie, but constrained to appear at the same time on both sides of the stimulus display to avoid the possible advantage of an attention switching strategy. Orientations were drawn uniformly from two sets of non-overlapping standards [11.25°, 56.25°, 101.25°, 146.25°] and [33.75°, 78.75°, 123.75°, 168.75°]. The standards were offset so that the same orientation was never present on both sides at once. The value for each side randomly varied so no orientation was associated with a side.

On all trials, eye position was recorded using an Eyelink II, 2.11 with 250Hz sampling (SR research, ON). The position of the right eye was recorded for all trials, and trials were included for analysis only if fixation was confirmed. When fixation failed, observers were alerted with five consecutive high frequency tones and the trial aborted. The percentage of aborted trials for each observer in each experiment ranged from 1.7% to 14% with an overall mean including all experiments of 5.7 ± 0.8%.

2.3.3 Analysis

Observers responded with one of four key presses that indicated likely-no, guess-no, guess-yes, or likely-yes. These ratings were used to form a receiver operating characteristic (ROC) function and performance was summarized as the percent area (A') under the ROC function. A' is equivalent to the percent correct measured by forced-choice paradigms (Green & Swets, 1966). To estimate A' we used the trapezoid method to avoid making distributional assumptions (Macmillan & Creelman, 2004) and converted to a percentage.

The difference in A' between the cue-one and cue-both conditions is our primary measure of the effect of divided attention. We refer to it as the *pre-cue effect* and interpret it as likely to be an effect of divided attention.

2.4 Experiment 1: Basic Change Detection

Our first experiment was designed to estimate the magnitude of the divided attention effect in a version of change detection that is typical of the literature (e.g. Keshvari, van den Berg, & Ma, 2013). This task consists of two stimulus displays separated by a blank. In each display, there was a stimulus on both sides of fixation. In the cue-one condition, if a change occurs it was restricted to the pre-cued side whereas in the cue-both condition the change could occur on either side and the observer made a single decision for the whole display. Given that the task is made up of two possible events that can map to the same response (a many-to-one mapping) this is sometimes called a compound task (Sperling & Dosher, 1986) and is commonly used in visual search. The difference between performance in cue-one versus cue-both conditions is the divided attention effect. No divided attention effect is expected if all processing stages are unlimited capacity (perception, memory and decision).

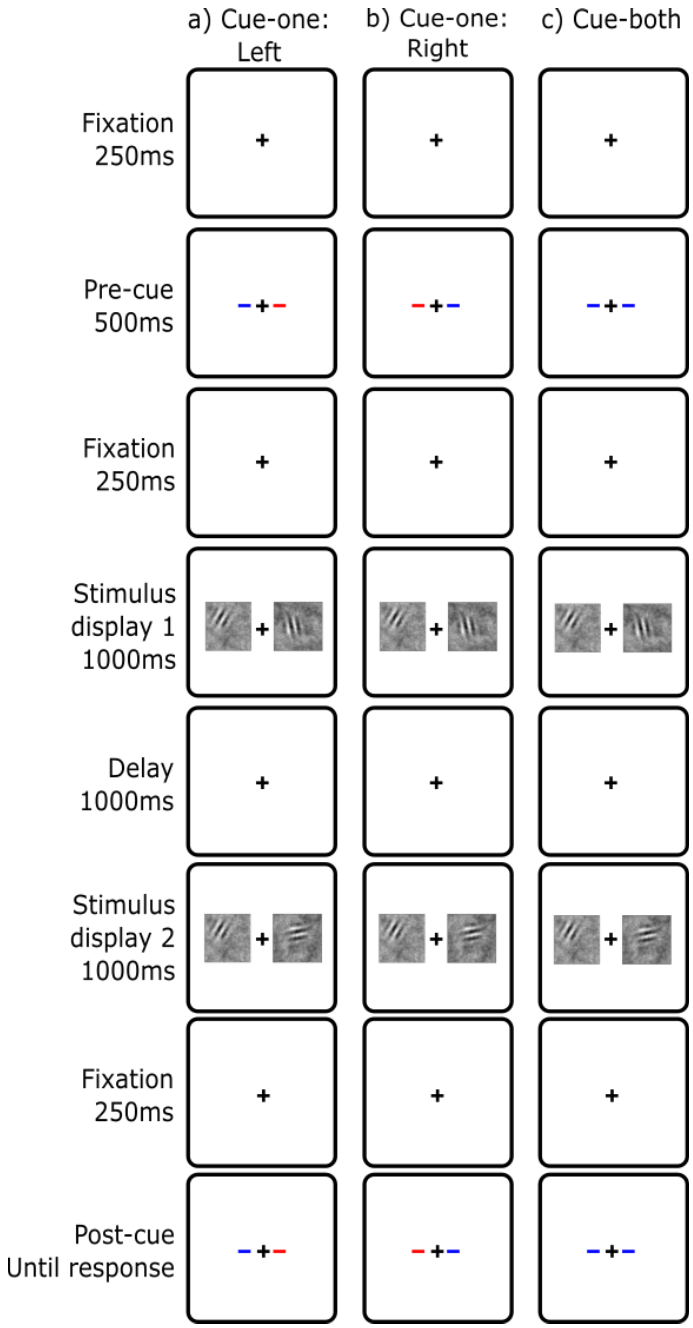


Figure 2-2. Display conditions of Experiment 1 basic change detection with blue as the cue color. a) Cue-one Left b) Cue-one Right c) Cue-both. Unlike this illustration, all experiments had the entire screen a middle gray rather than just the stimulus and noise as shown here.

2.4.1 Methods

The method was as described in the General Methods section. The specific task is shown in Figure 2-2 and proceeded as follows. The first and second stimulus displays contained a Gabor in both the left and the right side. On 50% of trials a change in orientation of 90° occurred on one of the relevant sides. In the cue-one blocks, the change could occur only on the pre-cued side, while the uncued side always remained unchanged in orientation. In cue-both blocks, the change could occur on either side but not both. The observer's task was to make a response as to whether a change had occurred on either side. Observers responded on a rating scale likely-no, guess-no, guess-yes, or likely-yes without having to specify which side contained the change.

2.4.2 Results

Performance in each cuing condition (collapsed across sides) are shown in Figure 2-3a. Performance was better in the cue-one condition (Mean = 80.1, SE = 0.9) than the cue-both condition (Mean = 72.2, SE = 1.1). This is a difference of 7.9%, 95% CI [5.7, 10.1], t(11) = 7.91, $p < .001$. This pattern of results was consistent across almost all observers (Figure 2-3b). Figure 2-3b plots the accuracy of each observer in the cue-both condition against their accuracy in the cue-one condition. Points falling below the identity line are observers performing worse in the cue-both condition relative to the cue-one condition.

There was also a significant effect of cuing on performance at high contrast, where performance was better in cue-one (Mean = 96.9, SE = 1.0) than cue-both (Mean = 93.3, SE = 1.5). This is a difference of 3.6%, 95% CI [1.5, 5.6], t(11) = 3.88, $p = .003$.

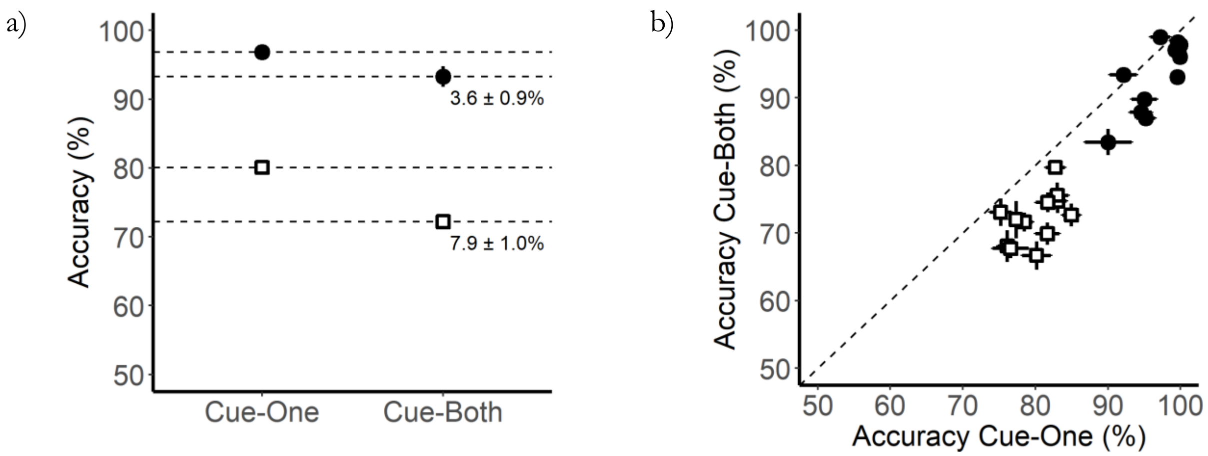


Figure 2-3. Results for Experiment 1 basic change detection. Low (open squares) and high (filled circles) contrast. a) Performance in cue-one and cue-both. b) Individual subject performance in a scatterplot of cue-one versus cue-both. Error bars are standard error of the mean.

2.4.3 Discussion

The results of our basic change detection are consistent with similar studies of divided attention in showing a divided attention effect (Keshvari et al., 2013; Luck & Vogel, 1997; Scott-Brown & Orbach, 1998). The results are not consistent with an account in which perception, memory and decision have unlimited capacity for two stimuli. Thus, even for two stimuli, one or more stages must be limiting performance with multiple stimuli.

2.5 Experiment 2: Post-cued Change Detection

In the next experiment, we addressed the role of decision in change detection. Simple change detection as in Experiment 1 includes dependencies across sides because different events can lead to the same response (e.g. a change on the left, or right will lead to a change response). This many-to-one mapping complicates the interpretation of the results because it obfuscates the source of information used in the decision (Braun & Julesz, 1998; Shaw, 1980; Sperling & Dosher, 1986). In the next experiment, we made each stimulus judgement an independent task (sometimes called a concurrent task or dual-task; Sperling & Dosher, 1986), and used a post-cue to indicate the response side. The task now has a one-to-one mapping between stimulus and response (illustrated in the schematic in Figure 2-4). If the result of Experiment 1 is due only to the effect of the compounded decision error then the effect should be eliminated in Experiment 2.

Furthermore, the stimulus displays for the cue-one condition can now be identical to the cue-both condition in that changes can occur on both sides independently with 50% probability. In this experiment, the only display difference between the in the cue-one and cue-both conditions is the pre-cue.

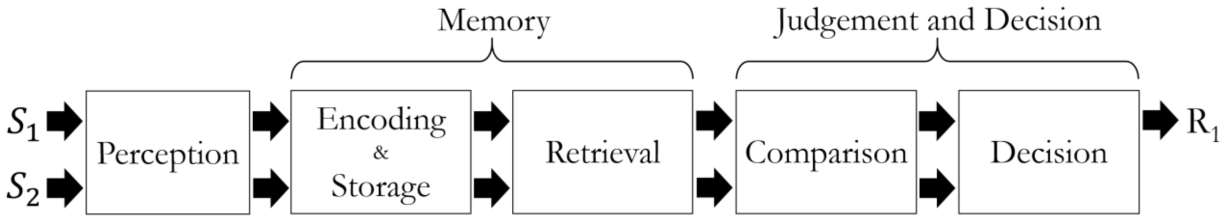


Figure 2-4. Schematic of the stages of processing for the post-cued change detection task. The response is only for the stimulus on one side.

2.5.1 Methods

The General Methods were used except that (1) the presence of a change is independent on the left and right side - changes occur on one or both sides in both the cue-one and cue-both conditions, and (2) observers must respond only to whether a change occurred within the post-cued side. The observer used two independent sets of response keys corresponding to the left and right side (but only one response is made on each trial).

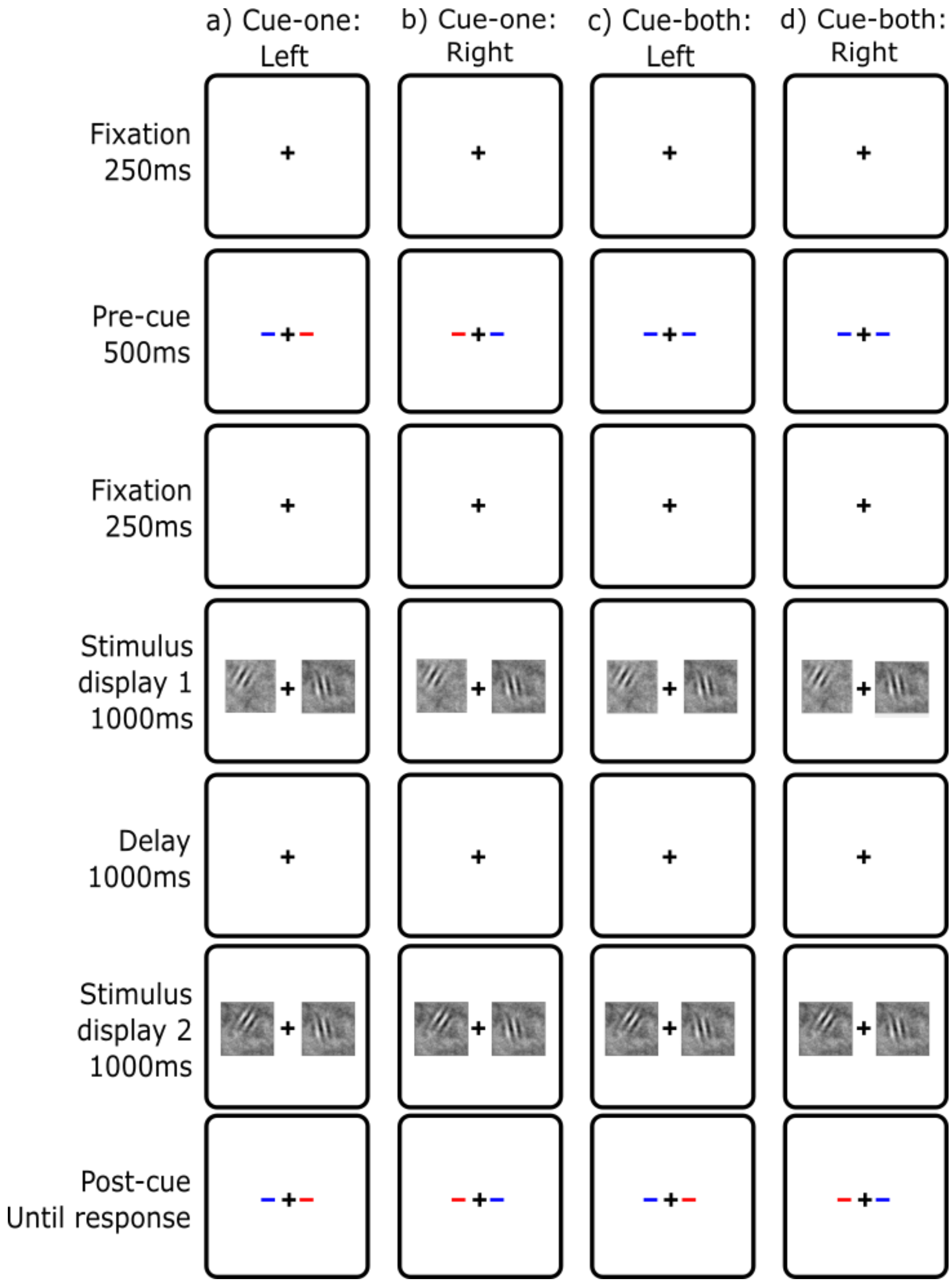


Figure 2-5. Display conditions of Experiment 2: Post-cued change detection, with blue as the cue color. a) Cue-one Left: The left side is pre-cued with 100% validity as the side that will be tested on this trial. b) Cue-one Right: The right side is pre-cued as relevant. c) Cue-both left: Both sides were pre-cued as potential response sides and the left side is later post-cued for response. d) Cue-both right: Both sides were pre-cued as relevant and the right side is later post-cued for response.

2.5.2 Results

Figure 2-6a plots A’ for each condition. Performance was better in the cue-one condition (Mean = 82.1%, SE = 1.3%) than the cue-both condition (Mean = 75.0%, SE = 1.7%). This is a difference of 7.1%, 95% CI [4.1, 10.1], $t(11) = 5.22$, $p < .001$. This pattern of results was consistent across almost all observers (Figure 2-6b).

There was also a significant effect of cuing on performance at high contrast, where performance was better in cue-one (Mean = 98.1, SE = 0.6) than cue-both (Mean = 91.0, SE = 1.8). This is a difference of 7.2%, 95% CI [3.9, 10.4], $t(11) = 4.9$, $p < .001$.

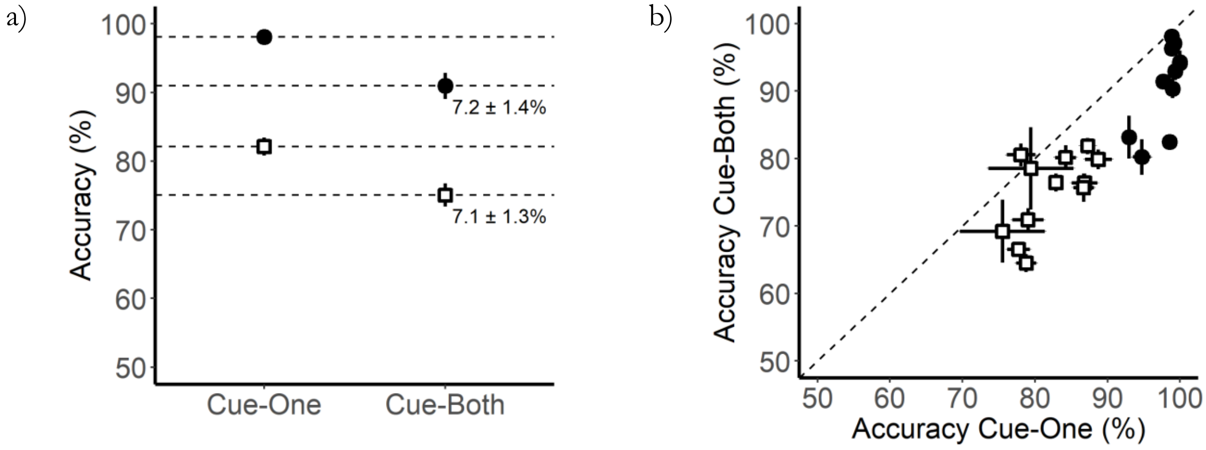


Figure 2-6. Results for Experiment 2: Post-cued Change Detection change detection. a) Mean performance in cue-one and cue-both for low (open squares) and high (filled circles) contrast. b) Individual subject performance in cue-one and cue-both.

2.5.2.1 CONGRUENCY

The results of dual task designs can be further deconstructed by the congruency of the stimulus events at each location on each trial. Congruent trials are ones in which the same stimuli event (e.g. a change) occurred at both locations. Incongruent trials are ones in which different stimuli events happened at each location (e.g. a change on one side, and not on the other). Effects of congruency would be evidence of dependencies across the two stimuli. However, we found there was no effect of congruency on performance (see Appendix).

2.5.2.2 *ORIENTATION SIMILARITY AND PERCEPTUAL GROUPING*

When two orientations are presented together they might form a single representation or "group" (Silvis & Shapiro, 2014). If such perceptual grouping occurs for our observers, then our task is not really be testing one versus two stimuli. Due to our selection of offset orientations, there was never identical orientations on both sides in a given stimulus display. However, there are still pairings that are arguably more conveniently grouped into either corners or almost parallel lines. Despite this possibility, we find no evidence of perceptual grouping or performance variations dependent on which orientation was presented (see Appendix for further details and discussion).

2.5.3 Discussion

When using a post-cue to limit the decision to include stimuli from only one side we still find an effect of the pre-cue. Observers' performance was higher when one side was pre-cued as relevant than when both sides were pre-cued. These results are consistent with the findings of Scott-Brown & Orbach (1998) where effects of a pre-cue were predicted by a decision noise account for contrast change detection task when the stimulus array were of uniform-contrast, but not when they were mixed-contrast. The decision noise account (Palmer, 1994) predicts no difference between these two conditions because only the number of stimuli is relevant. The observed effect suggests that while decision noise might play some role in change detection it cannot explain the full effect. The remaining effect of divided attention is therefore likely to be due to perception, memory encoding, storage, retrieval, or comparison. We next consider effects of memory and comparison.

2.6 Experiment 3: Retention-interval cue change detection

In Experiment 3, we consider whether effects before memory retrieval contribute to the effect. This experiment is a version of change detection identical to the post-cued change detection task of Experiment 2, except that a retention-interval cue (e.g. Griffin & Nobre, 2003) was inserted between the two stimulus displays. The retention-interval cue informed the observer the side on which they would later respond (i.e. it matched the post-cue). This task therefore required them to retrieve from memory only the orientation from the first display on the relevant side, and make a single comparison decision on the relevant side before responding. This is illustrated in the schematic in Figure 2-7.

Observers still had to perceive and encode the two stimuli from the first stimulus display and store them in memory until the retention-interval cue. Thus, Experiment 3 has the same perception, memory encoding and storage requirements as Experiment 2, but different memory retrieval and comparison demands. If perception, memory encoding, or memory storage of two orientations is the limiting factor then we expect the divided attention effect to persist with a retention-interval cue. If, however, memory retrieval or comparison is the limiting factor then the divided attention effect will be eliminated.

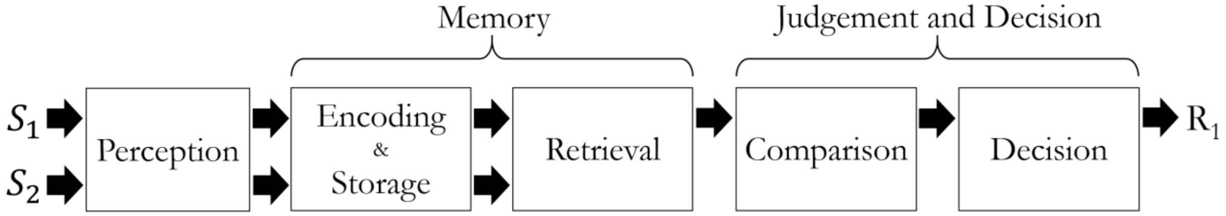


Figure 2-7. Schematic of the stages of processing for the post-cued change detection task. There is no continued processing beyond storage for the uncued side.

2.6.1 Methods

The stimuli in this experiment were identical to Experiment 2 except for the additional cue. The experiment consisted of two stimulus displays with the addition of a retention-interval cue, identical to the post-cue, between the displays. In the cue-one condition this new cue provided no additional information. In the cue-both condition, the observer knew earlier which side was relevant.

2.6.2 Results

Figure 2-8a plots A’ for each condition. There was no reliable difference between the cue-one (M = 79.3, SE = 1.1) and cue-both (M = 78.5, SE = 0.9) conditions. This is a difference of 0.8% 95% CI [-1.0, 2.5], t(11) = 0.97, *p* = .35. This was also the case in the high contrast version of the task (cue-one M = 98.0, SE = 0.6; cue-both M = 97.0, SE = 1.0, difference = 1.1, 95% CI [-0.2, 2.3], t(11) = 1.9, *p* = .10.

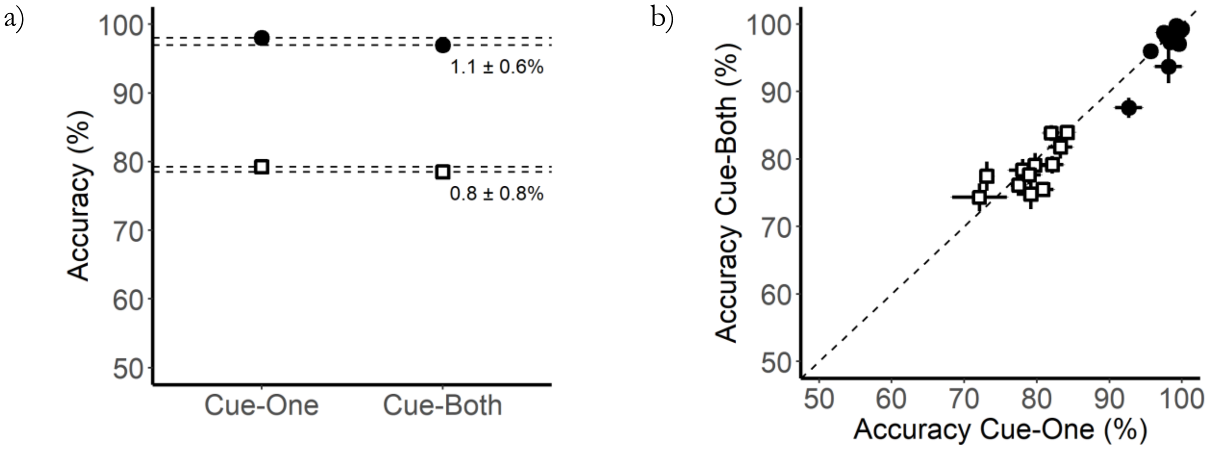


Figure 2-8. Results for Experiment 3: Retention-interval cue change detection. a) Performance in cue-one and cue-both for low (open squares) and high (filled circles) contrast conditions. b) Subject performance in cue-one and cue-both.

2.6.2.1 *STIMULUS TIMING*

For all experiments other than Experiment 3 the second stimulus and post-cue occurs beyond the time limits of iconic memory (Sperling, 1960). In Experiment 3 however, the retention-interval cue appears 250 ms after the end of the stimulus display. The Gabor could be present up to the last 200 ms of the stimulus display, resulting in the possibility that in some trials the retention-interval cue could appear within 450ms which is perhaps within the window of iconic memory (Becker, Pashler, & Anstis, 2000). It would then be possible for the observer to encode only one stimulus from the first display and lead to improved performance in the cue-both condition relative to other experiments. We examined performance as a function of the timing of the Gabor appearing in the noise and found no effect of the timing (see Appendix).

2.6.3 Discussion

The lack of divided attention effect in Experiment 3 suggests that there is no limit to dividing attention in change detection up to the point of memory retrieval and comparison. In other words, there is no limit in perceiving the stimuli and that memory encoding and storage are also unlimited capacity for two stimuli. Instead, the limiting process must be retrieval or comparison.

2.7 Experiment 4: Probe Recognition

Experiment 4 is similar to Experiment 3 in that the observer must make only one memory retrieval and comparison. This task presents a first stimulus display on both sides followed by a second stimulus display with only a stimulus on the response relevant side (Figure 2-9). By including this task, we test whether the introduction of the retention-interval cue had some unanticipated effect beyond acting as a retrieval cue. For example, it is possible that the retention-interval cue provided the relevancy information closer to the first stimulus display and could arguably cause a difference in encoding or storage (Vogel, Woodman, & Luck, 2006).

This paradigm is similar to experiments where a cue is presented simultaneously with the second (or test) stimulus display (simu-cue; e.g. Beck & van Lamsweerde, 2011; Hollingworth, 2003; Luck & Vogel, 1997; Makovski, Sussman, & Jiang, 2008; Wheeler & Treisman, 2002).

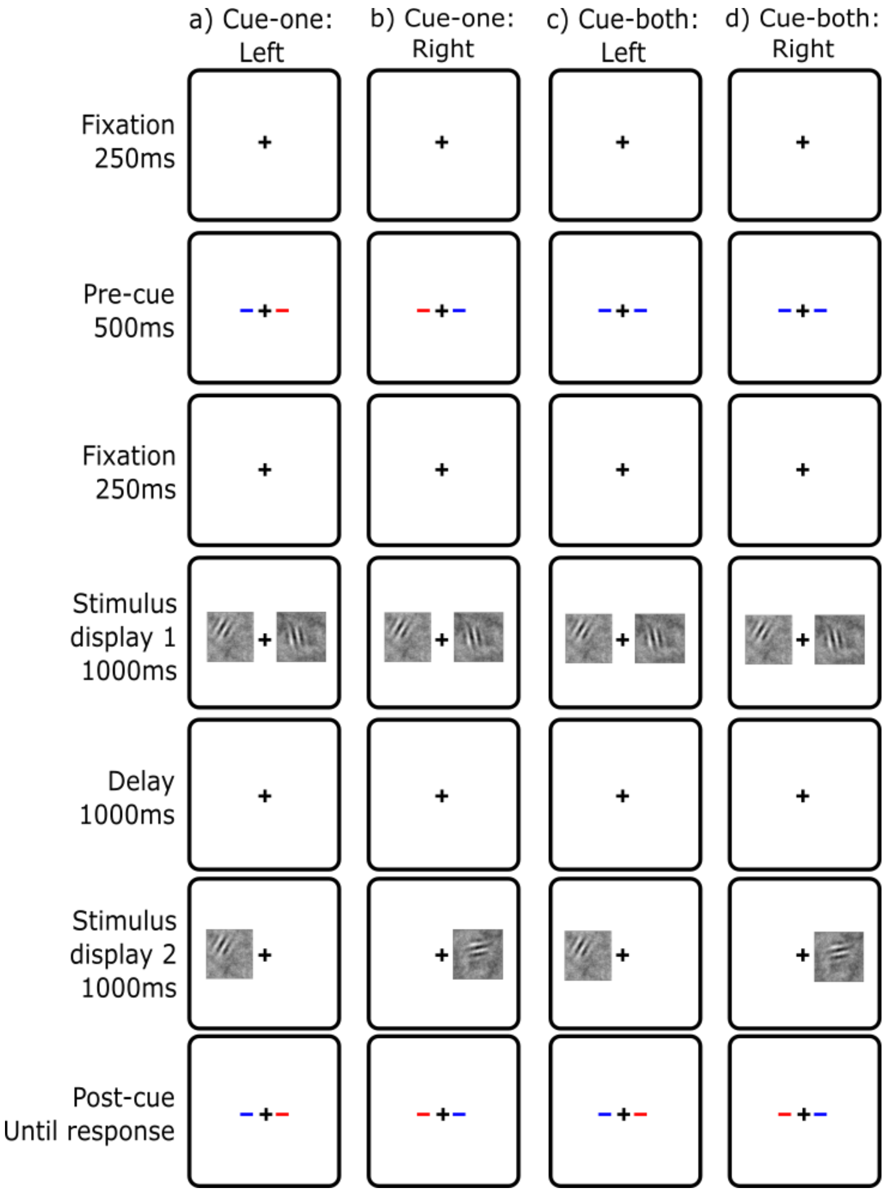


Figure 2-9**.** Display conditions of Experiment 4: Probe recognition, with blue as the cue color. a) Cue-one Left. b) Cue-one Right. c) Cue-both left. d) Cue-both right.

2.7.1 Methods

The stimuli were identical to Experiment 2 except the second stimulus display contained a stimulus on only the relevant side (Figure 2-9).

2.7.2 Results

Figure 2-10a plots A' for each condition. There was no reliable difference between the cue-one (M = 82.5, SE = 1.2) and cue-both (M = 80.8, SE = 1.5) conditions. This is a difference of 1.7% 95% CI [-0.1, 3.46], t(11) = 2.08, *p* = .06.

There was a small significant effect of dividing attention in the high contrast condition (cue-one M = 97.7, SE = 0.8; cue-both M = 96.5, SE = 1.1, difference = 1.2, 95% CI [0.4, 2.0], t(11) = 3.4, *p* = .006. This small effect is a the limit of what we can measure and is a fraction of the effects measured in the basic and post-cue experiments.

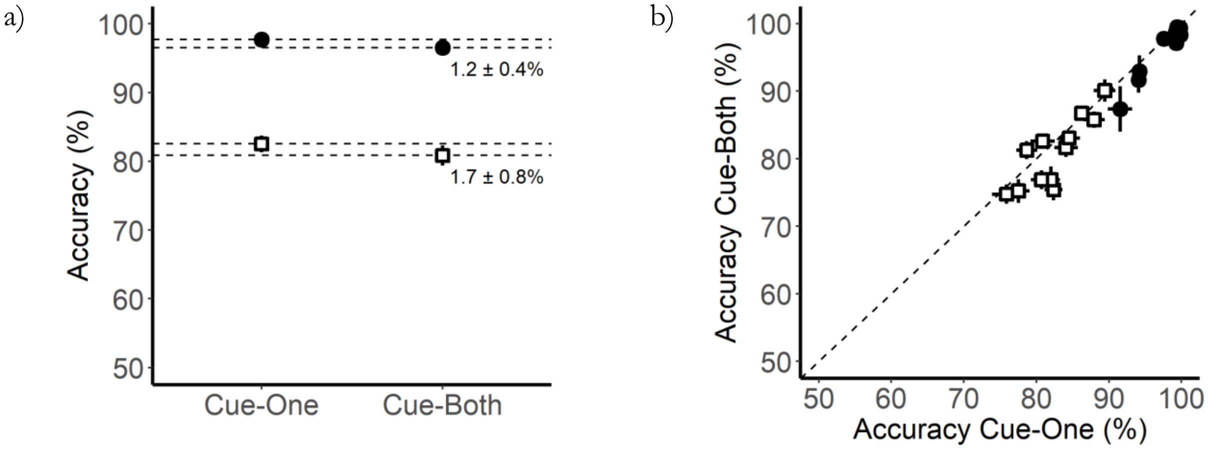


Figure 2-10. Results for Experiment 4: Probe recognition. a) Performance in cue-one and cue-both for low (open squares) and high (filled circles) contrast conditions. b) Subject performance in cue-one and cue-both.

2.7.3 Discussion

The results of Experiment 4 are consistent with the results of Experiment 3 showing that when only one retrieval and comparison must be made there is little or no divided attention effect. An alternative explanation for Experiment 3 was that retention-interval cue processing between the stimulus displays changed the encoding or storage processes in some way. Finding the same result for Experiment 4, which did not have the retention-interval cue, suggests that the effects of Experiment 3 were not due only to the processing of the cue between the stimulus displays and rules out an explanation based solely on a difference in encoding or storage (Williams & Woodman, 2012; Zhang & Luck, 2008).

2.8 General Discussion

2.8.1 Summary of Results

We measured the effect of divided attention in a variety of change detection tasks which are summarized in Figure 2-11. Considering first the results for low contrast stimuli (Figure 2-11A). For basic and post-cued change detection, we found a decrease in performance for two relevant stimuli compared to one. These two tasks required maintenance of relevant stimuli throughout perception, memory and decision stages of processing and so the performance decrement could be due to any one of these stages.

For change detection using either a retention-interval cue or probe recognition, we found nearly the same performance for two relevant stimuli as for one. These tasks differ from basic and post-cued change detection in that there are two relevant stimuli through perception, memory encoding and storage, but only a single relevant stimulus through memory retrieval and comparison. For the high contrast version, all of these experiments there was a qualitatively similar pattern of results for one versus two stimuli.

The results of the dual task manipulation can be further broken down by congruency of the stimuli events at each location on each trial. Congruent trials are ones in which the same stimuli event (e.g. a change) occurred at both locations. Incongruent trials are ones in which different stimuli events happened at each location (e.g. a change on one side, and not on the other). Performance in these two types of trials indicates the degree of independence across locations. If performance is independent then there should be no difference between congruent and incongruent trial performance. On the other hand, interactive processes, such as cross-talk, predict congruency effects (e.g. Bonnel, Stein, &

Bertucci, 1992). This would be indicative of another kind of divided attention effect beyond an accuracy difference across pre-cue conditions. Examples of congruency effects are found in a number of divided attention experiments (e.g. Navon & Miller, 1987).

Figure 2-12 in the Appendix shows the congruency effects in our experiments. There was no evidence of congruency effects across the two sides which is inconsistent with interactive processes in any of the processing stages.

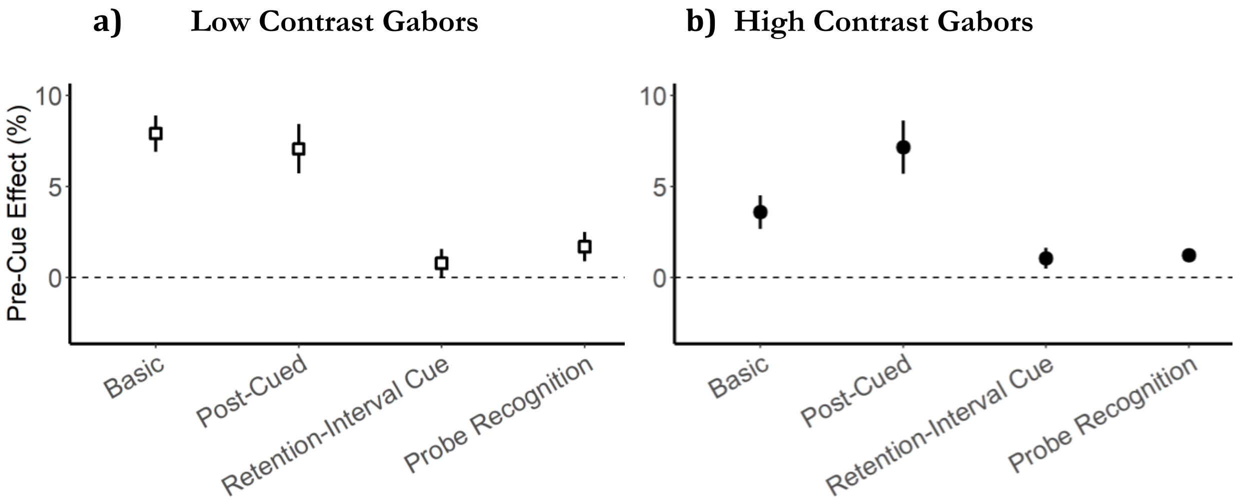


Figure 2-11. Magnitude of the pre-cue effect (cue-one minus cue-both) in each of the experiments in the low (a) and high contrast (b) conditions.

2.8.2 Implications for perception

By perception, we mean the immediate effects of the stimulus presentation that are distinct from delayed memory-based processes. It is challenging to separate effects of perception from effects of memory encoding and storage. In the experiments presented here it was unnecessary to pursue the distinction owing to the finding of unlimited capacity across all of these early processing stages.

Many change detection experiments vary the number of stimuli in the initial stimulus display and therefore change the sensory input from condition to condition which may introduce unintended effects, such as crowding (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001) which are not necessarily considered attentional effects. We avoided this confound by always having stimuli present on both sides of the display for our cue-one and cue-both conditions. This means that there was no change to the perceptual input, and rules out a simple perceptual account of the results such as crowding.

Finding no effect of the pre-cue for perception is consistent with results from detection or detection-like tasks (Bonnel et al., 1992; White, Runeson, Palmer, Ernst, & Boynton, 2017). These results differ from the many theories that posit a limited capacity in perception for divided attention tasks. At one extreme are theories suggesting a bottleneck that allows only one stimulus to be identified at a time (Broadbent, 1958), while other theories are less severe suggesting a limited resource that is divided among relevant items (e.g. Kahneman, 1973). These theories predict that performance in divided attention tasks is impaired because the stimuli are in competition for the limited processing resources in perceptual stages. One solution to these conflicting findings of limited and unlimited capacity for divided attention is a theory in which the outcome is dependent on the stimulus and task. Under come conditions, these theories predict unlimited capacity, and in other conditions they predict limited capacity (e.g. Hoffman, 1979; Scharff, Palmer, & Moore, 2011).

2.8.3 Implications for memory

Change detection in memory research primarily differs from the use for perception in the types of stimuli used. Rather than being perceptually challenging stimuli such as low contrast Gabors, or small luminance changes, memory research typically uses easily discriminable stimuli such as high contrast bars, colored patches or nameable objects. As an example of a change detection task for memory, Wilken & Ma (2004) briefly displayed arrays of squares with highly distinct colors, followed by a delay, and a second array. Within each trial, there was a .5 probability that one item would change in color from the first to the second array. The results show that as set size increases (N = 2, 4, 6, 8) the hit rate falls and false alarm rate rises.

In the memory literature, the use of attentional cues to specify relevant and irrelevant stimuli has become known as *directed forgetting*. For a review of this large literature see MacLeod (1998). Most of this work has been for verbal stimuli, but see Williams, Hong, Kang, Carlisle, & Woodman (2013) and Hourihan, Ozubko, & MacLeod (2009). Reviews emphasize three hypotheses to account for this kind of attentional effect in memory: selective rehearsal (Basden, Basden, & Gargano, 1993), retrieval inhibition (Bjork, 1989)or selective search in retrieval (Epstein, Massaro, & Wilder, 1972).

Memory encoding: Limited capacity at encoding means insufficient stimulus information is moved to storage. Sensory representations are retained only briefly after the stimulus event (e.g. Averbach & Coriell, 1961; di Lollo, 1980; Sperling, 1960) and therefore are unlikely to be encoded much beyond the first stimulus display of our task. The retention-interval cue and probe recognition effects suggest that the stimulus representations are successfully encoded into memory storage because they are available for later access. This is consistent with those who have found insensitivity to stimulus array duration (Cowan et al., 2005; Luck & Vogel, 1997; Sperling, 1960), or have otherwise argued against capacity limits in encoding (Rideaux et al., 2015; Rideaux & Edwards, 2016). This result is not compatible with serial encoding (Becker et al., 2013).

Memory storage. Limited capacity storage means that although both stimuli were encoded adequately into memory, the representations are not maintained sufficiently well for retrieval and comparison. Storage limits might be in terms of the number of items (e.g. Luck & Vogel, 1997) or of the quality of the representations (e.g. Keshvari et al., 2013).

Our experiments are inconsistent with a memory storage limit: if the items were not stored in memory then a retention-interval cue or probe would not be able to retrieve the relevant item and improve performance. Given that we see a no divided attention effect with the retention-interval cue and probe recognition is seems unlikely that there is a limit in storage for two items.

Other studies have argued for storage limits (Williams et al., 2013). In a typical directed forgetting task the observer is provided with a cue indicating which stimuli to forget. For example, Williams et al. (2013) presented one versus two colored squares and measured the precision recall for a probed item. Performance for two items was worse than for one but was improved when a cue indicated that one item could be forgotten (i.e. would not be probed). The authors use these results as evidence for limited capacity storage hypotheses such as selective rehearsal (Basden et al., 1993). This experiment is very similar to comparing our retention-interval cued change detection to probe recognition. However, unlike Williams et al. (2013) we see no difference between cue-one and cue-both for either of these tasks and therefore find no evidence for the limited capacity storage hypotheses.

Memory retrieval: Limited capacity in retrieval means that although both stimuli were encoded and stored adequately, the representations are not retrieved with sufficient information for successful comparison (Shiffrin, 1970). Our results are consistent with a limit in retrieval which has precedents in the literature. For example, in the case of the ability of observers to report features of stimuli despite failing to report a change event (Fernandez-Duque & Thornton, 2000; Hayhoe, Bensinger & Ballard, 1998; Henderson & Hollingworth, 2002; Hollingworth, Williams & Henderson, 2001). Retrieval limits have also been shown with natural scene change detection where the use of a probe to test single items in the scene improved performance relative to detecting a change anywhere in the scene (Hollingworth, 2003).

What might cause the retrieval failure? Some believe that the retention-interval cue stabilizes what is otherwise a volatile representation by some mechanism (e.g. retrieval inhibition: Anderson & Neely, 1996; Bjork, 1989), while others believe the context cue for retrieval from memory is the helpful mechanism (Oberauer & Lin, 2016).

These accounts clash with other accounts of working memory that assert no retrieval for the items held in the 'focus of attention' and that several items can be held in the focus of attention (Cowan, 2011; Cowan et al., 2005). Instead items are extracted directly from the sensory representation and have "direct access" for comparison to the second display (Cowan et al., 2005). If this 'direct access' account is accepted, then in our tasks, retrieval and storage are effectively amalgamated. This would imply that retrieval is not the limit in change detection leaving comparison as the limiting process.

2.8.4 Implications for comparison

The results with the retention-interval cue and probe recognition are also consistent with a limit in the comparison. Only one comparison has to be made in each of these conditions and performance was the same regardless of whether there was one or two stimuli that had to be perceived, encoded and stored in memory. This hypothesis is supported by results showing that despite failing to detect a change, a subsequent probe about stimulus identity demonstrates sufficient information was available (Angelone et al., 2003; Farell, 1985; Fernandez-Duque & Thornton, 2000; Hyun et al., 2009; Mitroff et al., 2004; Simons et al., 2002). For example, Mitroff et al. (2004) showed that, despite encoding sufficient information about all of the relevant stimuli for a 2AFC task asking whether items had been present in either display, observers still failed to detect changes. Findings such as this one have been interpreted as it being possible to retrieve the relevant stimuli from memory, but failing to make the correct comparison when there are multiple comparisons to be made. A flaw in this argument is that at the time of retrieval only one item is relevant, and so these results cannot distinguish between a retrieval limit and a comparison/judgement limit. An ideal experiment would independently manipulate the number of retrievals and the number of comparisons to distinguish between limits in each process.

2.8.5 Implications for decision

Decision noise describes the uncertainty in mapping an external stimulus to a discrete response. As the number of relevant stimuli increases, additional uncertainty from each stimulus is included in the decision which limits performance (Palmer et al., 2000; Sperling & Dosher, 1986; Swets et al., 1961). Change detection tasks are often structured such that set size increases and all stimuli contain relevant information that is integrated to make the decision. For example, in Experiment 1 observers were asked to detect a change occurring anywhere in the array, so that all locations are informative to the decision. In contrast, in Experiment 2 with a post-cue, observers only had to map a single stimulus to their judgement. However, we still saw an effect of the pre-cue suggesting that decision noise is not the source of divided attention effects in change detection for these conditions.

2.8.6 Generalization

In this article, we focus entirely on the case of orientation of Gabors, but all of our interpretation has assumed that this is not a special feature. Many papers using change detection use salient and highly discriminable colors as the feature and thus color would therefore be a natural direction to test for generalization. In favor of similarity between our stimuli and highly discriminable colors, we found the same pattern of results in our high contrast condition suggesting that our results are not due to limited visibility. The question of whether color is different from orientation is less clear. In a series of papers asking whether encoding into visual short-term memory occurs in series or in parallel, Becker and colleagues found color and orientation to be different (Becker et al., 2013; Liu & Becker, 2013; Mance, Becker, & Liu, 2012; Miller, Becker, & Liu, 2014). They compared performance in a probe recognition task when the to be encoded stimuli were presented simultaneously versus sequentially. If encoding proceeds in unlimited capacity parallel then there should be no difference between these conditions, but if the process is limited then performance should be better in sequential than simultaneous. They found that for color but not orientation the performance was equivalent between simultaneous and sequential suggesting that color, but not orientation, can be encoded in parallel for one versus two items. What do we make of the results? First, these results suggest that orientation and color can be processed differently within a similar task structure. Second, the serial result for orientation is inconsistent with our data. In a probe recognition task, we find unlimited capacity for two stimuli. The differences found by Becker and colleagues do not predict a different pattern of results for color in our task given that they find unlimited capacity parallel encoding for color.

Many visual memory studies focus on limits occurring at larger set sizes, such as two versus four stimuli. It is likely that additional limits are introduced with more stimuli. For example, crowding becomes a possible perceptual limit with more than a few stimuli (e.g. Parkes et al., 2001), and memory storage for more than two items also has been discussed extensively as a limit (e.g. Cowan, 2000; Landman et al., 2003; Luck & Vogel, 1997). How much of these effects are accounted for by the same limits we find for one versus two stimuli is a good question.

Our use of a coarse change of 90° means that there can be considerable loss in precision without any impact on accuracy. With a finer discrimination task, we might find that perception is not unlimited, and that precision decreases with one to two stimuli as others have (Keshvari, van den Berg, & Ma, 2012).

Our choice of stimuli may be dissimilar to the natural scenes used in some visual memory work, but the results are complimentary. For example, Hollingworth (2003) has shown the benefit of a retention-interval cue to a natural scene change detection task and suggested that retrieval is the limiting factor.

It might be less surprising that in a cluttered natural image that a retrieval cue can help as a context cue. It is perhaps more surprising that in a sparse simple feature display that the same effect can be demonstrated with a retention-interval cue.

2.9 Conclusion

We investigated the source of divided attention effects for change detection by varying when observers are cued to one of just two stimuli. For basic change detection, performance was worse when there are two relevant stimuli than when there is a single relevant stimuli. This pattern persisted for a post-cued change detection. But when a retention-interval cue between the stimulus displays indicated the relevant stimulus, performance for two versus one was nearly the same. This was also true of an experiment that used probe recognition to test a single stimulus. We conclude that the limiting process in change detection with just two stimuli is in the memory retrieval and/or the comparison processes. Perception, memory encoding and storage are ruled out as the limiting processes for these conditions. Thus, retrieval and comparison processes are critical to understanding divided attention in change detection.

2.10 Appendix: Further analyses of all experiments

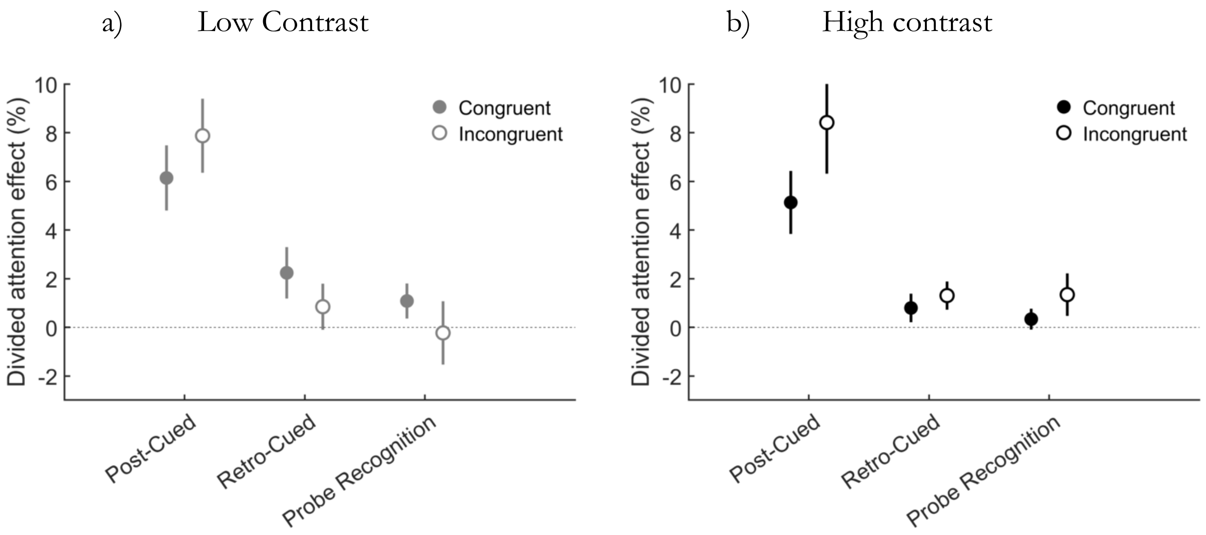
2.10.1 Stimulus timing

To test the possibility that stimulus timing affected performance we correlated the timing of the stimulus in the first stimulus display with the performance in that trial. If the presence of the stimulus in iconic memory at the time of the retention-interval cue was of benefit then we would expect performance to improve the later in the trial the Gabor was presented (i.e. a positive correlation). None of our observers showed a significant correlation (mean correlation coefficient = .01, $p > .05$ with bonferroni correction) in Experiment 4 or any other experiment.

2.10.2 Congruency

The results of dual task designs can be further broken down by congruency of the stimuli events at each location on each trial. Congruent trials are ones in which the same stimuli event (e.g. a change) occurred at both locations. Incongruent trials are ones in which different stimuli events happened at each location (e.g. a change on one side, and not on the other). Performance in these two types of trials indicates the degree of independence across locations. If performance is independent then there should be no difference in performance between congruent and incongruent trial. On the other hand, if there is a dependency across sides then there might be a difference between these trial types (e.g. Bonnel, Stein, & Bertucci, 1992). This would be indicative of another kind of divided attention effect beyond an accuracy difference across pre-cue conditions. Examples of congruency effects have been found in a number of divided attention experiments (e.g. Navon & Miller, 1987).

The results separated by congruency for the three dual task experiments (Experiments 2-4) are shown in Figure 2-12. There was no reliable effect of congruency in any experiment or contrast condition.


a) Low Contrast

b) High contrast

Figure 2-12 Congruency results for post-cued change detection, retention-interval cued change detection and probe recognition at (a) low and (b) high contrast.

2.10.2.1 ORIENTATION SIMILARITY AND PERCEPTUAL GROUPING

There are several findings that suggest perceptual grouping did not play a significant role in the present experiments. First, performance was no better or worse in probe recognition than with the retention-interval cue. We might expect that by removing the reference of the second side stimulus in probe recognition that we have removed any benefits of perceptual grouping because the context has changed. This would predict a smaller divided attention effect in retention-interval cued change detection. However, the divided attention effect was similar in these two experiments suggesting that perceptual grouping was not improving performance in the retention-interval cued cue-both condition relative to the probe recognition cue-both condition.

Second, if certain groupings of orientations were more conducive to grouping then we might expect to see differences between these pairs. There were two possible differences between angles on the two sides (22.5° and 67.5°) and the mean performance was the same in each case (22.5°: mean = 86.1, se = 0.4; 67.5°: mean = 86.1, se = 0.4). A three-way ANOVA 4 (experiment) x 2 (contrast) x 2 (orientation distance) found main effects of experiment and contrast but not of orientation difference, F(1, 179) = 0.71, *p* = .40.

Third, when the side of the change is not relevant, as in Experiment 1, perceptual grouping might improve performance if any stage of perception, memory or comparison was limited because it is only the one grouped item that must be encoded, stored and retrieved for comparison. Any change in this item from the first to the second stimulus display would be reported as a change. By making the locations independent in Experiment 2 this strategy is less helpful. The magnitude of the divided attention effect was similar in Experiment 1 and 2 suggesting that perceptual grouping was not helpful as a strategy for reducing the number of items.

Why might we not see any perceptual grouping effects? Any benefit of perceptual grouping of the orientations might have been elliminated due to the randomized location of the stimuli from first to second stimulus display or due to the presence of noise.

2.10.2.2 Observer Participation

Observers participated in different combinations of experiments. Table 2-1 indicates experiments in which each observer participated.

Table 2-1 Experiments in which each of the 19 observers participated. Zeros indicate non-participation.

Observer	Experiment			
	1: Basic	2: Post-Cued	3: Retro-Cued	4: Probe Recognition
1	1	1	1	1
2	1	1	1	1
3	1	1	1	1
4	1	1	1	1
5	1	1	1	1
6	1	0	1	1
7	1	0	1	1
8	1	0	1	1
9	0	1	1	1
10	1	0	1	1
11	0	0	1	1
12	1	1	0	0
13	0	1	0	1
14	1	1	0	0
15	0	0	1	0
16	0	1	0	0
17	0	1	0	0
18	0	1	0	0
19	1	0	0	0

Chapter 3. Effects of dividing feature-based attention on fMRI BOLD responses in visual cortex

James C. Moreland & Geoffrey M. Boynton

University of Washington

3.1 Abstract

In visual cortex, feature-based attention enhances neural responses with receptive fields at the stimulus location, but these enhanced responses also extend to receptive fields beyond the relevant location. When only one feature is task relevant, the spread of activity across space can facilitate perception of behaviorally relevant stimuli. However, when multiple features are relevant, what is the effect on behavior and brain activity? Behaviorally, we observed reduced performance when attending to two relevant features compared to just one relevant feature. Measuring the responses to specific components of the stimulus using fMRI we found larger responses to the attended components but that these effects were much larger when attention was directed to the same feature at two locations than two different features at the two locations. Our fMRI results in area hMT+ can predict our behavioral results by extending the normalization model of attention to include a global feature-based attention component that leads to suppressed responses to attended stimulus components when attention is directed to opposing directions of motion.

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3.2 Introduction

Feature-based attention can select relevant features such as colors or directions of motion from the visual field irrespective of the spatial position (e.g. Boynton 2009; Martinez-Trujillo and Treue 2002; McAdams and Maunsell 1999). In human visual cortex not only do we see feature-based activity acting at the location of an attended stimulus, but that activity also spreads to stimuli beyond the spatially relevant location (Saenz et al., 2002).

When only one feature is task relevant, the spread of activity across space can act to facilitate perception of behaviorally relevant stimuli (e.g. all red stimuli). However, when multiple features are relevant across multiple stimuli (e.g. red for one stimulus and blue for another), what is the effect on behavior and brain activity? A common approach to studying this question has been to have two feature values overlapping at two locations and ask the observer to attend to one feature value at each location (Andersen et al., 2013; Lo et al., 2012; Saenz et al., 2002, 2003; Serences & Boynton, 2007a). For example, Saenz et al. (2003) presented two overlapping fields of dots in apertures at two spatial locations. In each aperture, one field of dots moved upwards and the second moved downwards. Under these same physical conditions, two attention conditions were compared. In the first, the observers made psychophysical judgements on the field with the same feature (e.g. up). In the second condition, the judgements were made on fields with different features at either location (e.g. up left, down right). When the same feature value was relevant at both locations, performance was better that when a different feature values were relevant at each location (see also Andersen et al., 2013). These behavioral results suggest that it is not possible to enhance two features independently at each location and support a hypothesis that feature-specific activity is not spatially constrained even when it would be advantageous to the task to do so. A second experiment by Saenz et al. (2003) suggests that the dependence relates to the presence of the conflicting feature at the same location. When only one feature value was present at each location there was no difference in performance for same versus different features (see also Experiment 2 of Lo et al., 2012). This suggests that there is not only a feature-specific enhancement across the visual field but also some interference from irrelevant stimuli that share another target's feature value.

These divided attention effects have also been observed in the brain using EEG. Steady-state visually evoked potentials (SSVEP) measured the responses to features at different locations and found enhanced activity for the when the same feature value was relevant at two locations relative to when conflicting feature values were relevant (Andersen et al., 2013, 2015; Forschack et al., 2017). This effect was greatly reduced, or eliminated, when the irrelevant features did not share feature values with relevant stimuli. These results suggest that there is feature-specific enhancement across the visual field but reduced responses to irrelevant features are specific to distractors and targets sharing feature values.

In the present study, fMRI responses were measured in the visual cortex while subjects divided attention between two locations (left and right of fixation) of moving dot stimuli, each containing overlapping upward and downward motion fields. In one condition, subjects divided attention across the two locations and performed a task on two fields moving in the same direction. In a second condition, attention was divided across space to opposite directions of motion. We replicated previous behavioral results using similar stimulus conditions and found that performance is better when attention is divided to the same feature than when dividing attention to different features (Andersen et al., 2013; Saenz et al., 2003). These behavioral results suggest that it is not possible to enhance the response to two features independently at two locations.

We applied an inverted encoding approach to our fMRI results (IEM: Brouwer and Heeger 2009; Foster et al. 2017; Sprague and Serences 2013) to examine the effect of attention on the response to each of the four dot fields. This approach enables a quantification of the population response to each of the two directions of motion at each of the two spatial locations. Our results show an overall larger response to the two attended stimulus components, replicating previous studies of spatial and feature-based attention. However, consistent with our behavioral results, in areas V3 and hMT+ these attentional effects were much larger when attention was directed to the same directions of motion than opposing directions. Our fMRI results in areas V3 and hMT+, but not earlier visual areas, can be predicted by an extension of the normalization model of attention which incorporates a spread of feature-based attention across space and a normalization process that suppresses responses to opposing motion directions.

3.3 Methods

Methods were preregistered with the open science framework prior to data collection and can be accessed here: https://osf.io/hjm75/

3.3.1 Participants

Seven healthy subjects (including author JM) with normal or corrected to normal vision were recruited from undergraduates and graduate students at the University of Washington. All subjects provided written informed consent and received \$20/hr compensation (other than the author JM) for their behavioral participation and \$30/hr for fMRI participation. Subjects completed 1-2 (number determined by reaching a level of acceptable performance) behavioral sessions lasting one hour, and 2-3 fMRI sessions each lasting 1-1.5 hours.

3.3.2 Stimuli and procedure

3.3.2.1 BASIC STIMULI

Each stimulus component was a circular aperture of dots placed to the left and right of fixation (location parameters: 3.5° radius, centered ±6° away horizontally and -2.75° vertically) moving either upward or downward (dot parameters: white 100% luminance; speed 5°/s; 0.25° diameter; limited lifetime of 12 frames; 100% direction coherence) (Figure 3-1B). The display background was set at 30% of max luminance. Displays could contain one (forward model scans) or all four (divided attention task) component fields of moving dots (Figure 3-1C). Because all the dots were the same color within the aperture, the only cue for segmentation was the motion direction.

3.3.2.2 DIVIDED ATTENTION TASK

Figure 3-1A shows a schematic of the procedure applied during single trials for both fMRI and behavioral experiments. The stimulus display consisted of four fields of moving dots. Two overlapping in each aperture – one moving upwards and one moving downwards. The observers' attention was directed to individual fields using arrows cuing a single field on each side (dual-task) as relevant to a luminance decrement detection task. The arrows could indicate fields that are moving in the same direction (*attend-same*), or in opposite directions (*attend-different*). There were four combinations of dot fields which could be cued as relvant per trial: left up (LU) right up (RU), left down (LD) right down (LD), LULD, and LDRU. Importantly, this task manipulated the attentional state of the observer while keeping the physical stimulus, eye position and spatial distribution of attention identical. Trials were completed as blocks of five trials of the same attention condition (e.g. left up, right up). Each attention condition block was completed once per scan for a total of 20 trials per scan.

Target events are defined as brief luminance decrements (from max screen luminance to background luminance of 30%, occurring in a Gaussian temporal window with SD = 200 ms) in the trial's relevant fields. Distractor events are defined as luminance decrements of the dots in the trial's irrelevant fields. On each 14 s stimulus presentation there were variable numbers of target and distracter events to ensure that the observer maintained attention throughout the trial and not only until they thought all target events had occurred. Events were randomly interleaved and spaced at least 750 ms apart with the first event occurring at least 500 ms after the dot onset and the last event ending 500 ms before the dot offset. It was made clear to the observers that the events were randomly timed and were independent across fields.

The subject began by foveating a fixation point on the center of the display and were required to maintain fixation on this point throughout the entire trial. At the start of each trial an arrow (1250 ms; 1° horizontal and 2.75° vertical displacement from fixation) on each side of the display indicated the relevant field directions for that trial. After a brief delay (500 ms), the moving dots stimulus was initiated and continued for 14 s. The observer's task was to press a button when they detected a target event. Responses for a left field were made with the left hand, and responses to a right field were made with the right hand. The next trial will began after a blank inter-trial interval of 2 s. Trials were grouped in sets of 5 within an attention condition block. There was 10 s between each block. There was a total of 20 trials in each scan (394 s scans including a 4 s time before the first trial). The order of attention conditions was randomized within scans.

During training, feedback was given in the form of the fixation point turning green for correctly detecting (Hit) a luminance decrement in a relevant field and pressing the corresponding response key within 1 s. When an event was incorrectly detected or a response was made on the wrong side then the fixation point would turn red. In the behavioral only session, feedback was used until performance was at > 70% hits. Feedback was also used prior to beginning a scan session to remind observers of the task.

During practice in the laboratory, the stimuli were generated and displayed via CRT monitor with a 120 Hz refresh rate while eye position was recorded using an Eyelink II, 2.11 with 250Hz sampling (SR research, Ottawa, Ontario, Canada). During sessions conducted in the scanner, the stimuli were generated using a Dell XPS 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).

3.3.3 FMRI data acquisition

fMRI data was acquired in a Phillips 3T Achieva MRI 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 with a repetition time of 2 s and echo time of 30 ms. Eighteen axial slices (80 x 80 matrix, 22-mm field of view, no gap) will be 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. From each subject we collected six standard retinotopic mapping scans, six forward model scans, and eight experimental scans across three scan dates.

3.3.4 Forward model scans

MRI sessions included scans in which the observer viewed single fields of moving dots in isolation (left up, left down, right up, right down; Figure 3-1C), which were used to estimate each voxel's responses to each stimulus component separately for use in the inverse encoding procedure. Each dot field was presented 4 times for 10 s with 8 s blanks between field presentations. The order of conditions was randomized. Throughout these scans, observers performed a fixation dimming detection task. This encouraged the observer to hold a stable fixation, and maintain their attention at the fixation point.

3.3.5 Behavioral analysis

Observers made button presses when they detected luminance decrements in relevant fields. Responses were classified as hits, selection errors, misses, and false alarms. A hit was defined as a button press within one second of an event occurring in the relevant field on the same as the button. A selection error was defined as a button press made within one second of a distractor event, or a target event occurring on the opposite side to the button press. A miss was defined as no button press within one second of an event in a relevant field. A false alarm was defined as a button press when no event of either kind had occurred in the previous second.

Behavioral performance was assessed as rates of each of the four types of outcomes. We compared the rates of each kind of outcome across attention condition using an ANOVA with subject as a random effect.

3.3.6 fMRI analysis

We used standard phase-encoding retinotopic mapping procedures to define visual areas V1, V2, V3 and V4 (Engel, Glover, & Wandell, 1997). These areas were further restricted to regions of interest (ROIs) using the forward model scans. This choice of localizer is not circular with the main analysis because voxels identified with the spatial localizer are not be biased by any attention condition to be examined in the experiment. hMT+ was defined as a contiguous group of voxels lateral to the parietal-occipital sulcus and beyond the retinotopically organized visual areas that exhibited a large response to the moving dot stimulus versus blanks.

All preprocessing (anatomical-functional coregistration, slice-scan time correction, motion correction, and linear trend removal) was performed using BrainVoyager. We then imported preprocessed fMRI voxel time courses into Matlab for analysis with custom software. We applied GLMdenoise version 1.1 (Kay, Rokem, Winawer, Dougherty, & Wandell, 2013) to improve the signal-to-noise in our data using noise regressors derived from task-unrelated voxels. The results with and without GLMdenoise were compared using reliability measures orthogonal to the conditions of our experiments and GLMdenoise proved to be more reliable and so all further fMRI results used GLMdenoise voxel timecourses.

3.3.6.1 EYE MOVEMENTS

Our fMRI analysis relies on voxels representing the same spatial region throughout the experiment. This means that our observer's ability to fixate well was paramount. Prior to scanning, observers underwent training to fixate and minimize eye movements. During the scans, we measured eye position which we used to assess observer's fixation quality and discard trials in which their eye movements were excessive.

From the experimental scans, trials were excluded when more than one second out of the 14 second stimulus duration was spent outside of a 2° radius around fixation. One subject's was outside of the fixation ring for one second or greater on 62% of trials in one of their scan sessions, on this basis we did not have enough data in all of the attention conditions leading to the exclusion of this session from further analysis. For the remaining subjects, of the 120 trials each subject completed, 11% ±

5.7% were excluded from each subject. Exclusion of trials was implemented by regressing out that trial.

By comparison, in the single field scans, only 1.0% ± 0.6% of trials had periods greater than one second outside of fixation. During these scans the observer's task was to detect luminance changes in the fixation point rather than in the fields because we wanted to keep attention off of the stimulus fields. It seems that observers were better able to maintain fixation under these conditions. This can explain why we find relatively high reliability in the single field voxel weights and more noisy weights in the attentional weights.

3.3.6.2 INVERTED ENCODING PROCEDURE

We employed an inverse encoding procedure to estimate population responses, within each ROI, to each of the two spatial locations and directions of motion. The forward encoding model assumes that each voxel contains subpopulations of direction selective neurons, and that there is an uneven balance in the overall direction and spatial selectivity of neurons contributing to a given voxel's response (Kamitani & Tong, 2006). Using our fMRI responses we characterize a voxel's overall direction sensitivity as a weighted sum of the four hypothetical channels (left side moving up, LU; left side moving down, LD; right side moving up, RU; right side moving down, RD). The first stage of this analysis uses fMRI data recorded while viewing displays of single fields of moving dots in isolation (LU, LD, RU, RD) to estimate weights of each voxel to motion direction and location. In the second stage, the fMRI data from the divided attention experiment was used with the estimated "channel weights" from above to estimate the response to each stimulus component, using linear regression under the assumption that the pattern of response our stimulus components is a linear combination of the responses measured to each stimulus component alone. The four regression weights serve as estimates of each channel's response to each of the four stimulus components.

We employed an inverse encoding procedure to estimate responses to separate populations of neuronal ‘channels’ that are selective to each spatial position and direction of motion based on the pattern of fMRI responses across voxels.

The procedure operates in three stages. The first stage is to estimate each fMRI voxel’s sensitivity to each of the two locations and two directions of motion.

For each ROI, we assume that there is a “spatial channel” for each direction of motion. Each channel is composed of a set of neurons that responds to motion at its preferred location. The response strengths to the left-up, left-down, right-up and right-down channels are denoted C_{LU}, C_{LD}, C_{RU} and C_{RD} respectively**.** Each voxel i’s response D is a weighted sum of the four channel responses:

$$D_i = W_{iLU}C_{LU} + W_{iLD}C_{LD} + W_{iRU}C_{RU} + W_{iRD}C_{RD} + \text{noise}$$

Weights $W_{iLU}, W_{iLD}, W_{iRU}$ and W_{iRD} describe how strongly the four channels drive voxel i. We estimated these weights as the mean localizer scan responses to single fields which evoke unit responses to the channel related to the presented field and zero to all other channels. For example, for a left-up single field $C_{LU} = 1, C_{LD} = 0, C_{RU} = 0, C_{RD} = 0$.This results in a v-by-4 matrix W of voxel weights, where v is the number of voxels, and there is one column for each channel. Each condition of the divided attention experiment produced a v-by-1 vector D of voxel responses. The encoding model can then be expressed as:

$$D = WC + noise$$

Linear regression gives the best-fitting estimate of C, a 4-by-1 vector of channel responses:

$$\widehat{C} = \left(W^T W\right)^{-1} W^T D$$

On each trial, two fields were attended (one on each side) and two fields were unattended (one on each side). There were also two kinds of same trials (LURU, LDRD) and two kinds of different trials (LURD, LDRU). In our analyses we collapse across these pairs of fields and pairs of attention trials to give us channel weights for same-attended, same-unattended, different-attended, and different-unattended.

For each of our five regions of interest (ROIs: [V1, V2, V3, V4, and hMT+]), in each of our subjects we obtained channel weights in each of the four attention conditions (attend LURU; attend LDRD; attend LURD; attend LDRU). After collapsing across scans, this resulted in a four factor balanced data set: 7 (subject) x 5 (ROI) x 4 (weights) x 4 (attention condition) with ROI as a within-subject factor.

We hypothesized to find two results in a visual area containing motion information supporting the behavioral results. First, we expected that (1) channel weights associated with the two attended stimulus components are larger than for the two unattended components – a main effect of attention, and (2) we expected a greater difference between attended and unattended channel weights for *attend-same* than the *attend-different* conditions – an interaction between attention and attention condition. We tested this by collapsing the 4 (channel weights) x 4 (attention condition) matrix of channel weights for each ROI and subject into 2 x 2 matrix of values (attend vs. unattended channel X *attend-same* vs *attend-different* attention condition). For example, the attended channel *attend-same* condition is the average of the left up and right up channels for the attend left up, right up condition, and the left down and right down channels for the attend left down, right down condition. The unattended channel *attend-different* condition is the average of the left down, right up channels for the attend left up, right down condition and the left up, right down channels for the attend left down, right up conditions. Thus, the 7x5x4x4 set of channel weights collapses to a 7 (subject) x 5 (ROI) x 2 (attended vs. unattended) x 2 (same vs. different) data set.

We ran a 2x2 ANOVA with ROI as a within-subject measure to test for (1) a main effect of attended vs. unattended, (2) a main effect of *attend-same* vs. *attend-different* condition and (3) an interaction between attended vs. unattended and *attend-same* vs. *attend-different*. Planned comparisons included simple effect ANOVAs for each ROI, again testing for the two main effects and interaction.

3.4 Results

3.4.1 Behavioral results

Subjects performed a dual-task detecting luminance decrements on two fields Figure 3-1. The fields were either moving the same direction or different directions. Luminance decrement events could either be correctly reported as present in a relevant field (hit), not reported in a relevant field (miss), reported when occurring in an irrelevant field (selection error – SE), or reported when not present in any field (false alarm – FA).

3.4.1.1 BEHAVIOR ONLY SESSION

Figure 3-2 (a - c) shows the results of the behavioral task during laboratory behavior sessions. There was no difference between *attend-same* and *attend-different* conditions for hit rate (*attend-same* M = 0.85, SE = 0.04; *attend-different* M = 0.84, SE = 0.05) and false alarms (*attend-same* M = 0.002, SE = 0.0006; *attend-different* M = 0.003, SE = 0.001) (hit rate: F(1, 6) = 0.48, *p* = .51, η^2 = .97; false alarm rate: F(1, 6) = 0.47, *p* = .52, η^2= .60). There are three kinds of selection errors: responses made when an event occurred in the relevant location but in the irrelevant field, responses made when an event occurred at the irrelevant location in the relevant feature value, and responses made when an event occurred in an irrelevant location and irrelevant feature value. These error types were analyzed in an ANOVA with attention condition and selection error type (2 x 3 within subject). There was no overall effect of attention condition F(1, 30) = 2.43, p = .13, a significant effect of type F(2, 30) = 23.89, p < .001 and no significant interaction F(2, 30) = 1.98, p = .16. Planned simple effects comparisons for each selection error type showed a significant difference in error rate for only events occurring in an irrelevant field a relevant direction F(1,6) = 8.05, p = .03, η^2 = .91.

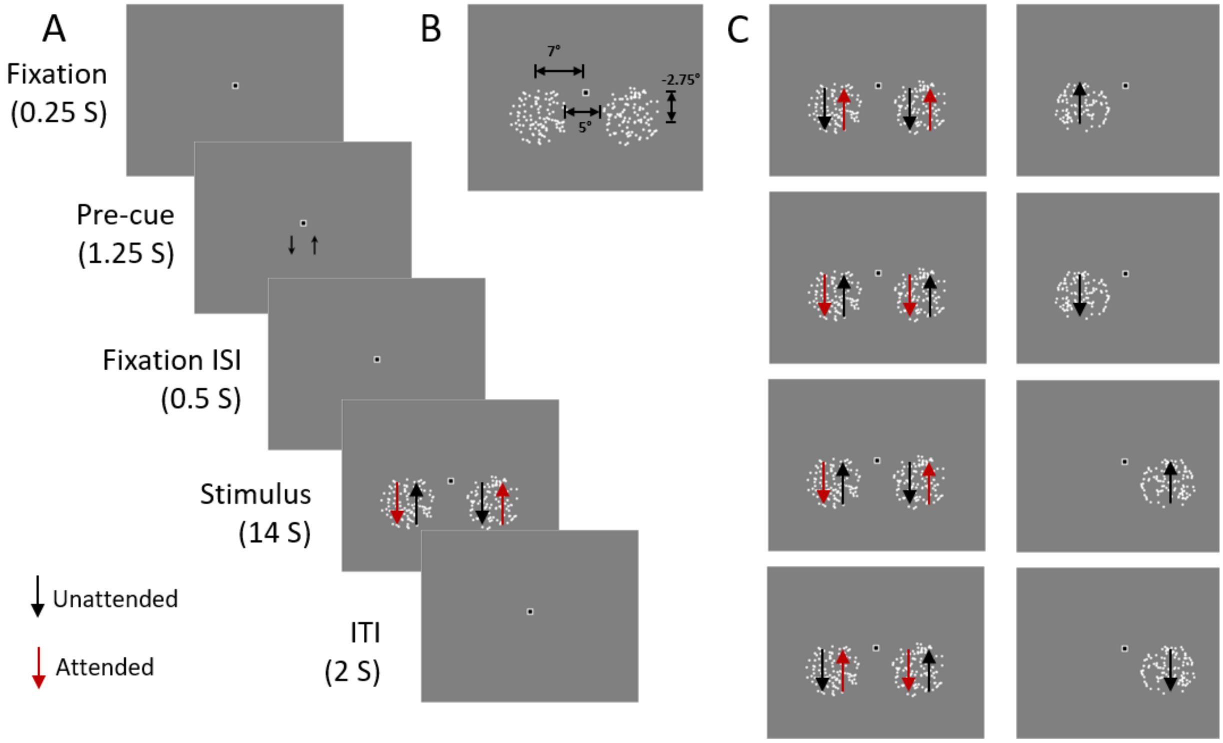

Figure 3-1 A) Schematic of an example trial in the divided feature attention task. The pre-cue could direct the observers to either field (up or down) on each side. There were no arrows on the stimulus display, these are included to indicate the directions of the four fields and the red indicates the relevant fields on this example trial. B) Stimulus size. C) Left column: Attention conditions. Red arrows indicates the relevant fields in each condition. Right column: Single field conditions used in forward model scans. There are no red arrows because attention was directed to a fixation task.

3.4.1.2 BEHAVIOR IN THE SCANNER

Figure 3-2 (d - f) shows the results of the behavioral task during scanning sessions. As in the laboratory, one-way ANOVAs with subject as a within factor found no difference between *attend-same* and *attend-different* conditions for hit rate (*attend-same* M = 0.86, SE = 0.05; *attend-different* M = 0.84, SE = 0.05, F(1,6) = 1.93, p = .21, η^2= .98) or false alarms (*attend-same* M = 0.004, SE = 0.001; *attend-different* M = 0.007, SE = 0.03, F(1,6) = 1.25, p = .31, η^2= .6). The three types of selection errors (see above) were included in an ANOVA with attention condition. There was no overall effect of attention condition F(1, 30) = 1.85, p = .18, a significant effect of type F(2, 30) = 22.12, p < .001 and no significant interaction F(2, 30) = 1.74, p = .19. As in the behavioral only session a planned simple effects analysis showed this to only be significant for events occurring in an irrelevant field in a relevant direction, F(1, 6) = 7.37, p = .03 , η^2 = .91.

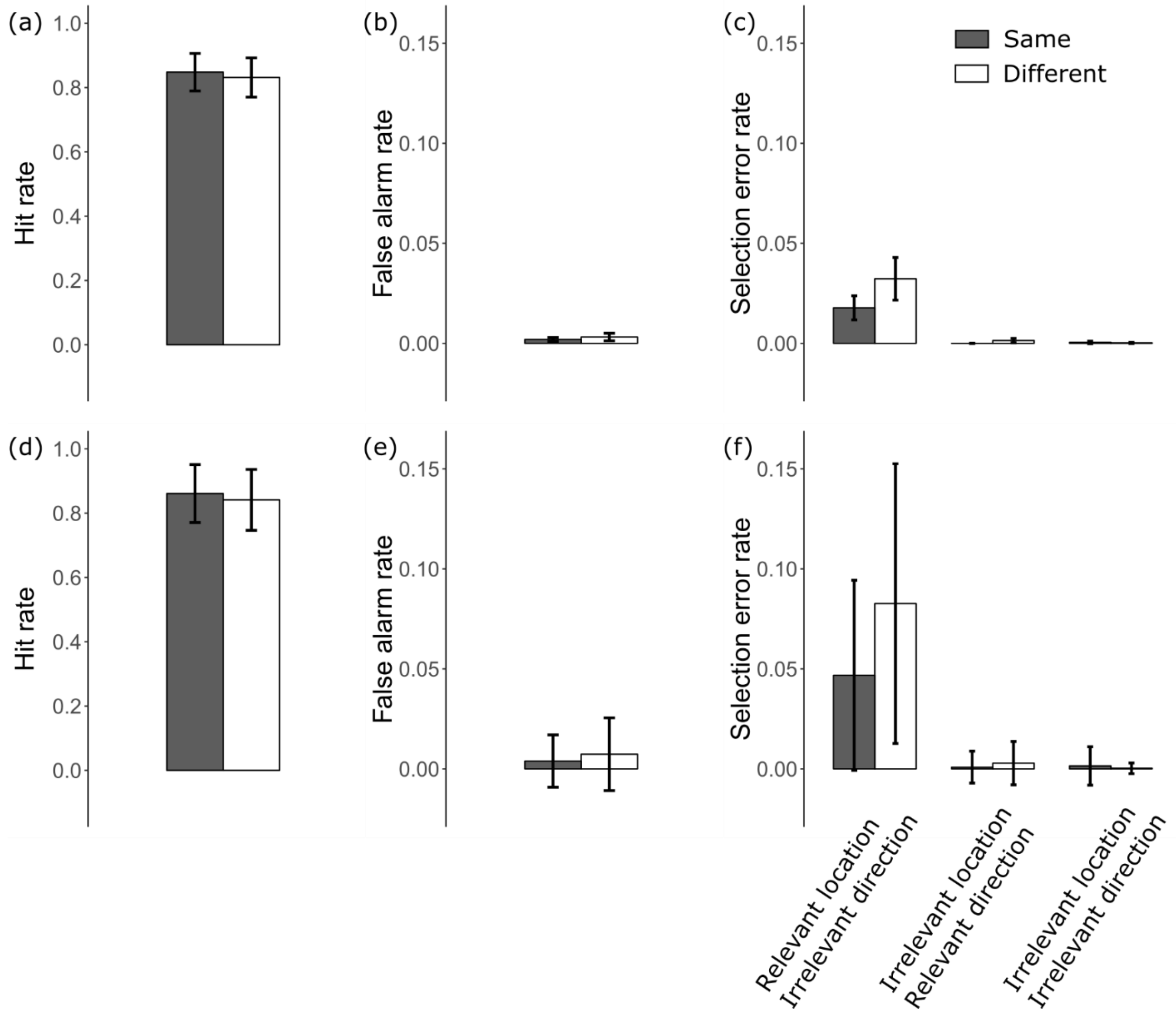

Figure 3-2. Results of behavioral task in behavioral only session (a-c) and in scanner sessions (d-f). Columns from left to right: Hits, False Alarms and Selection Errors. There are three kinds of selection errors. With respect to the side on which the button press was made, responses made when an event occurred in the relevant location but in the irrelevant field, responses made when an event occurred at the irrelevant location in the relevant feature value, and responses made when an event occurred in an irrelevant location and irrelevant feature value. Error bars are standard error of the mean across subjects.

3.4.2 fMRI results

On each trial, two fields were attended (one on each side) and two fields were unattended (one on each side). There were also two kinds of same trials (LURU, LDRD) and two kinds of different trials

(LURD, LDRU). In our analyses we collapse across these pairs of fields and pairs of attention trials to give us channel weights for same-attended, same-unattended, different-attended, and different-unattended.

Figure 3-3 shows the channel weights from the inverse decoding procedure in each area showing the response to the attended and unattended stimulus component for each of the two attention conditions. We used a 2 (field: attended vs unattended) x 2 (attention condition: *attend-same* vs *attend-different*) ANOVA (ML) with ROI as a within subject factor with subject as a random effect. We found a main effect of field, no main effect of attention condition, but an interaction of field with attention condition (field: F(1, 102) = 15.0, *p* < .001), attention condition: F(1, 102) = 0.48, *p* = .49), interaction: F(1, 102) = 6.45, *p* = .01)).

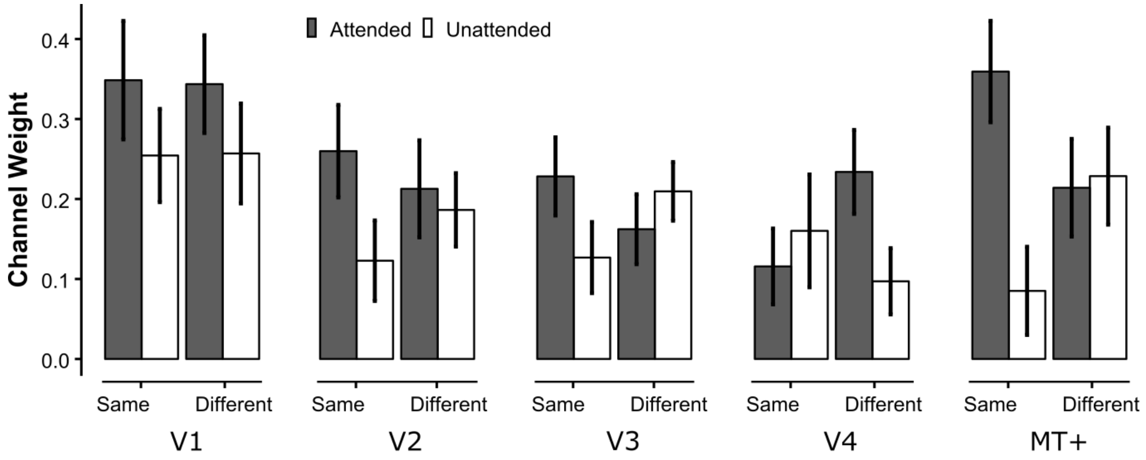

Figure 3-3. Channel weights for attended and unattended fields in the same and different conditions, for each visual area.

We carried out planned simple effects ANOVAs for each area separately, we found only areas V1 and hMT+ had near- or significant main effects of field (F(1, 18) = 4.37, p = .05; F(1, 18) = 8.01, p = .01).

No areas showed a main effect of attention condition. Areas V3 and hMT+ had significant interactions between field and attention condition (F(1, 18) = 6.20, p = .02; F(1, 18) = 10.4, p = .005).

This interaction between field and attentional condition is particularly strong in area hMT+, which shows a large attentional effect for the *attend-same* condition but no attentional effect for the *attend-different* condition. These channel responses in areas V3, and hMT+ are consistent with our behavioral results showing better performance for the attend same condition than the *attend-different* condition if we assume a signal-detection theory model in which performance on the motion task at a given spatial location is improved by both increased responses to the attended field, and decreased responses to the unattended field. Channel responses in area V1, show no interaction between field and attentional condition. These results would predict the same behavioral performance across the two conditions, inconsistent with our behavioral results.

3.4.3 Normalization Model

We can predict the pattern of results in areas V1 and hMT+ using a modification of the normalization model of attention (Lee & Maunsell, 2009; Reynolds & Heeger, 2009), which is an extension of the general normalization mechanism suggested for cortical processing to account for effects of attention on neuronal responses (for review see Carandini & Heeger, 2012). Figure 3-4 shows predicted responses when the excitatory drive is affected by attention in three ways. Model 1 (left column) is with no effect of attention on the excitatory drive (discs are uncolored). Model 2 (middle column) has spatial and feature-based attention operate independently, so only the attended two component responses are enhanced. We assume without loss of generality that in the *attend-same* condition, subjects are attending to upward motion on the left and the right. For the *attend-different* condition, subjects attend to up on the left and down on the right. Discs are saturated green for the two attended stimulus components and uncolored for unattended components for both conditions. Model 3 (right column) implements global feature-based attention for which the effect of feature-based attention spreads across space. For the *attend-same* condition, the excitatory drive is increased only for the two upward moving fields. For the *attend-different* condition, attention to upward motion on the left spreads to the upward component on the right, and similarly, attention to downward on the right spreads to modulate the excitatory response to downward on the left.

The next stage of the model computes the inhibitory drive, which is the excitatory drive summed across neurons tuned to all directions but with similar receptive field locations. In this illustration the inhibitory drive is the sum of responses across the two directions of motion for each spatial location. For model 1, there is weak excitatory drive for both directions and locations, so the inhibitory drive is also weak. For model 2, the inhibitory drive is intermediate, since it reflects the sum of the strong excitatory response to the attended component and weak excitatory response to the unattended component. Since spatial and feature-based attention are independent, the inhibitory drive is the same for both the *attend-same* and *attend-different* attention conditions. For Model 3, the inhibitory drive is also moderate for the *attend-same* condition. However, the inhibitory drive is strong for the 'different' condition because of the strong excitatory drive for both directions of motion.

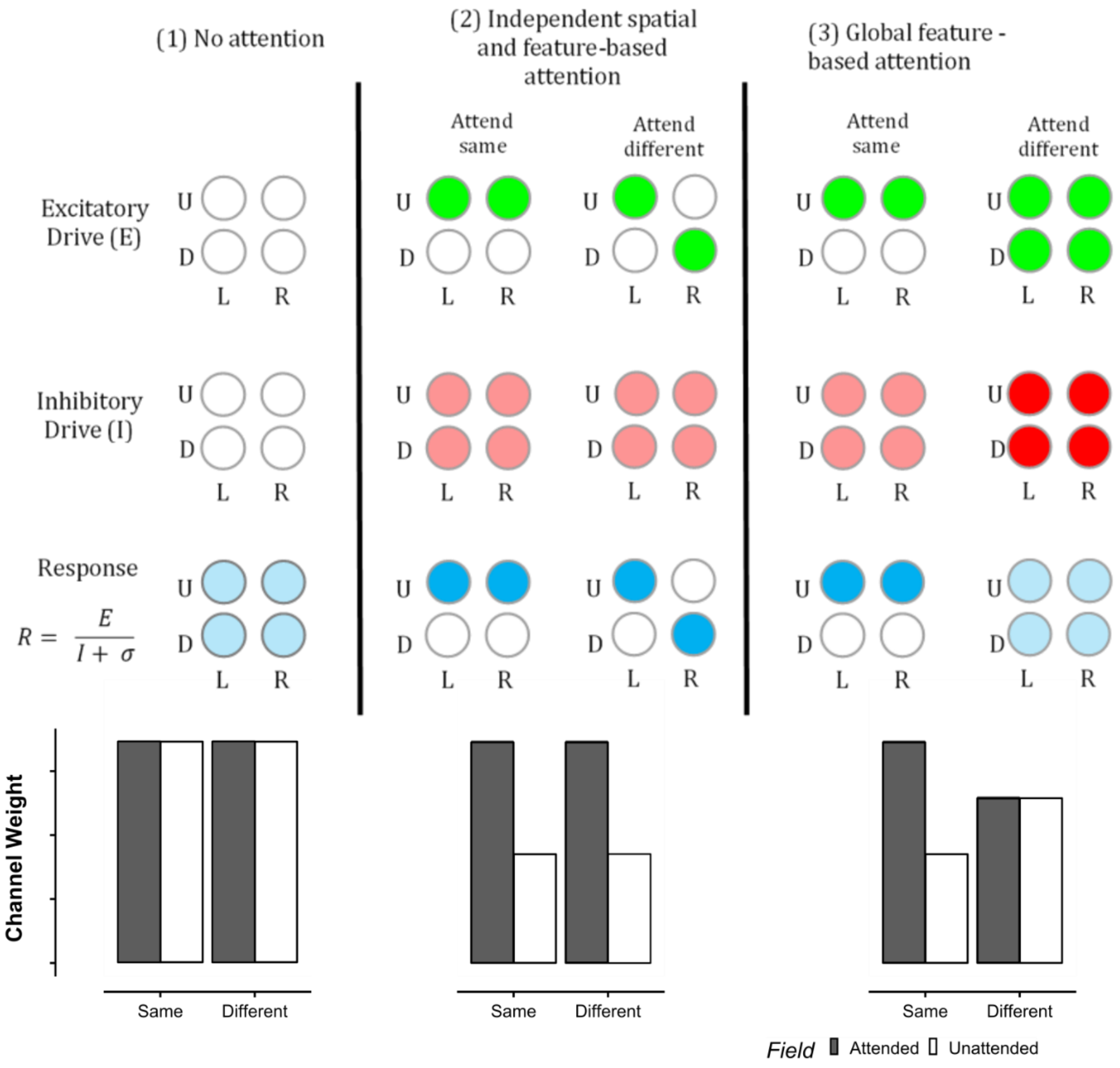

Figure 3-4 Illustration of three implementations of how the normalization model of attention can predict the effects of attention on neuronal responses. Discs represent responses to each of the four stimulus components (upward and downward motion in the left and right). The saturation of the color of each disc represents the strength of the response to that stimulus component along each stage of the model. Bottom row: Predicted channel weights from the normalization model of attention for each model.

The normalization model posits that the response in a population of neurons is the ratio of an excitatory drive, E, and inhibitory drive, I (plus a small constant, σ, to prevent infinite ratios). Spatial and feature-based attention only directly affects the excitatory drive – the rest of the processing in the model is the same, so that any effects of attention on the final responses are due to differences in excitatory drive.

The final stage essentially calculates the ratio of the excitatory drive and the inhibitory drive. Each of the three models predicts a distinct pattern of results. For model 1, the response is intermediate and equal for all four stimulus components, since this reflects the ratio of two weak responses. For model 2, if the effects of spatial and feature-based attention are independent, the response is large for the two attended stimulus components and weak for the two unattended stimulus components, reflecting the excitatory drive since the inhibitory drive does not vary across conditions. For model 3, with global feature-based attention, the effects of attention for the *attend-same* condition are the same as for model 2. However, the four responses for the *attend-different* condition are all intermediate and the same, due to the equal strength of the excitatory drive across stimulus components.

These model predictions can be sorted by whether the components are attended or unattended, and whether they came from the *attend-same* or *attend-different* condition to produce predicted channel weights that can be compared to our results. Figure 3-4 shows predicted channel weights for the three models. Model 1, with no attention predicts no difference between same and different conditions and no effect of attention within these conditions. Model 2, with independent spatial and feature-based attention predicts that attended components have a larger response than unattended components but that there is no difference between *attend-same* and *attend-different* conditions. Model 3, with global feature-based attention shows an effect of attention in the *attend-same* condition but not in the *attend-different* condition.

Predicted responses from the three models can be sorted by attended and unattended components for the *attend-same* and *attend-different* conditions to predict channel weights for comparison to our fMRI results. Comparing the three model predictions to our fMRI results in Figure 3-3, it can be seen that our results in area V1 resemble Model 2, which has independent spatial and feature-based attention, and results in area hMT+ are consistent with Model 3, which incorporates global feature-based attention.

Model 3 predictions, and area hMT+ results are consistent with our behavioral results, which supports the hypothesis that neuronal responses in area hMT+ are used to 'read-out' the information needed to perform our divided attention task.

3.5 Discussion

Behaviorally, we found that observers were able to detect events equally well when attending to different features at different locations as when attending to the same feature at the two locations. However, overall performance was compromised in the different feature condition by selection errors made within the same spatial location from the irrelevant stimulus field.

Our fMRI data supported a difference between same versus different feature conditions. Overall, feature-based responses were greater for the relevant than the irrelevant fields. But there was a difference in the magnitude of this attention effect depending on whether the observer was attending to the same versus different field directions. When attending to the same direction, there was a larger response in the attended fields and a smaller response in the unattended field resulting in a larger difference between attended and unattended fields. These overall effects were driven by areas V1, V3 and hMT+, which were the only areas to show the same effects when analyzed separately.

These divided attention effects have been observed previously using EEG. SSVEPs measured the responses to features at different locations and found enhanced activity for the when the same feature value was relevant at two locations relative to when conflicting feature values were relevant (Andersen et al., 2013, 2015; Forschack et al., 2017). This effect was greatly reduced, or eliminated, when the irrelevant features did not share feature values with relevant stimuli. These results suggest that there is feature-based enhancement across the visual field but reduced responses to irrelevant features are specific to distractors and targets sharing feature values.

We see that there is only a significant difference for selection errors within the same spatial location between same and different conditions. This source of performance error was not clear in previous work where either percent correct from discrete trials (Saenz et al., 2003), or aggregated selection errors and false alarms (Andersen et al., 2013) were reported. This type of error is consistent with evidence that behavioral performance is only impaired when the distractors at each location match the relevant feature at another location (Andersen et al., 2013; Lo & Holcombe, 2014; Saenz et al., 2003). It seems that for selection of two features, the challenge is suppressing the attended feature at irrelevant locations, and failures result in selection errors.

Previous neuroimaging results have suggested the spread of feature-based attention beyond the relevant spatial location by showing feature related responses in regions outside of the physical stimulus (Saenz et al., 2002; Serences & Boynton, 2007a). Consistent with this, we find greater responses in the irrelevant fields when the attended direction is different on each side. This suggests that feature-based attention acts across the visual field, which has the consequence of increasing responses to irrelevant fields sharing the same feature value.

The spread of feature-based activity across space has been described as a top-down gain control mechanism which appears as a baseline increase in neural activity for neurons preferring the relevant feature (Hayden & Gallant, 2009; Serences & Boynton, 2007a). While a gain mechanism can explain increased responses across space to relevant features, it does not immediately account for the differing responses for one versus two features. The reduction in the responses to relevant fields under the different attention condition might be explained by a limited capacity mechanism where a limited resource is divided between the relevant features resulting in a lower response. This theory makes an additional prediction that if the directions of motion were different in all four fields that the response to the relevant fields would be the same as in the two feature experiment. Other work suggests that this is not the case. Andersen et al. (2013) show that the response to the relevant feature is not reduced for two features when the irrelevant stimuli do not share features with the relevant stimuli. This is also reflected behaviorally in experiment 2 of Lo & Holcombe (2012) where performance for two relevant features was only reduced when the relevant and irrelevant stimuli shared features.

Instead, we propose a simple extension to the normalization model of attention (Lee & Maunsell, 2009; Reynolds & Heeger, 2009). In addition to the spatial effect of attention, an effect of feature attention can be introduced by implementing increased activity across the visual field for relevant feature values. This method can predict the pattern of results we find in V3 and hMT+ without having to add further parameters for capacity limits for dividing attention across feature values. Our results are not consistent with the pattern of results predicted by a normalization model with no effect of attention, or only spatial attention.

We only observe an interaction between field and attention condition in areas V3 and hMT+. A simple explanation for this might be that they are classically considered motion sensitive regions (Braddick et al., 2001; Britten, Shadlen, Newsome, & Movshon, 1992). However, area V1 is similarly sensitive to motion (Mikami, Newsome, & Wurtz, 1986; Movshon & Newsome, 2018) and did not display these effects. V1 and hMT+ differ in their responses to overlapping motion where only neurons in MT are suppressed in the presence of motion in the non-preferred direction in a manner that appears divisive (Snowden, Treue, Erickson, & Andersen, 1991). If feature-based attention acts to enhance the non-preferred direction then this increases the activity in the pool of neurons that will suppress the response to the relevant feature. This divisive normalization of motion directions may not occur in earlier visual areas. A proposed role for this difference in motion processing between V1 and MT is noise reduction and segmentation of different moving objects (Born & Bradley, 2005).

Reduction in responses during feature-based attention tasks with competing stimuli has be observed previously (Chapman & Störmer, 2018; Forschack et al., 2017; Müller, Gundlach, Forschack, & Brummerloh, 2018). Converse to global feature-based enhancement, feature-based suppression is thought to act locally to the relevant stimuli. For example, Forshcack et al. (2017) used SSVEP to determine the effect of feature-based attention on irrelevant stimuli in the periphery versus at the location of the relevant stimulus. They found that effects of feature enhancement could be detected in peripheral features matching the relevant feature value but there was no evidence of reduced responses in the periphery for the irrelevant feature value. We are not able to distinguish between local and global reduction in feature-based responses, as the predicted results in our experiment would be the same. However, in hMT+ it is likely that some voxels included neurons with receptive fields large enough to encompass both aperture locations. This would rule out a hypothesis of spatially isolated feature-based selection at least in area hMT+.

Some studies have found evidence of feature-based attention in visual areas that we did not, such as V4 (Motter, 1994; Bichot, Rossi & Desimone, 2005; Buracas & Albright, 2009). Instead, we find an effect of feature-based attention in V3 where others did not (Serences et al., 2009). This is perhaps due to the attribute used in each study. It seems that the areas found to be sensitive to effects of feature-based attention are related to the attribute relevant in the task. V4 is more sensitive to color and shape, where V3 and hMT+ are more sensitive to motion.

3.6 Concluding remarks

The present results show the effect of dividing attention across features on behavior and on responses in visual cortex. Our behavioral results show that it is more difficult to divide spatial attention to two different directions of motion than to the same direction of motion. Our fMRI results in area hMT+ are consistent with these behavioral results by showing a larger effect of attention when dividing attention to the same direction of motion than to different directions of motion. Our fMRI results can be predicted by a simple extension of the normalization model of attention, which incorporates a global spread of feature-based attention across space, followed by normalization process that pools responses to all directions of motion.

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