

GLOBAL ENHANCEMENT OF TASK-IRRELEVANT DIMENSIONS OF ATTENDED OBJECTS

BY

AUDREY GARDNER LUSTIG

THESIS

Submitted in partial fulfillment of the requirements
for the degree of Master of Arts in Psychology
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2011

Urbana, Illinois

Master's Committee:

Associate Professor Diane Beck, Chair
Associate Professor Monica Fabiani

ABSTRACT

Experiments on the neural mechanisms of feature-based attention suggest that features are selected in parallel across the visual field (Treue & Trujillo, 1999). Moreover, feature-based attention spreads not only to the task-relevant feature in an unattended location, but also to a task-irrelevant feature when it is bound to the task-relevant feature in a task-irrelevant location (Sohn et al., 2005). We asked whether a similar mechanism is at work when the task-irrelevant feature is bound to the task-relevant feature at the attended location. Specifically, we asked whether attending to the color of moving dots in one visual field (VF) would influence the motion signal to colored moving dots in the other VF.

Subjects attended to either red or cyan dots (both present in the upper right quadrant of the VF at the attended location and moving in opposite directions) and responded when the target dots dimmed. Critically, the color and motion of dots present in the upper left quadrant of the VF varied as a function of the attended dots such that they were either the same color/same direction, same color/opposite direction, opposite color/same direction, or opposite color/opposite direction as the attended dots.

We found main effects of both color and direction in areas of ventral visual cortex responsive to the task-irrelevant location, such that BOLD activity was greater when either the dots' color or direction were the same as the attended stimulus. We also found a main effect of direction in human MT/MST responsive to the task-irrelevant location, such that activity was greater when the dots in the task-irrelevant and task-relevant locations were moving in the same direction than when they were moving in opposite directions. These results support the theory that object-based attention leads to enhanced selection of all dimensions of the attended object, including task-irrelevant ones. Additionally, our findings suggest that this co-selection modulates the object's dimensions independently throughout the visual field via a feature-based mechanism.

TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION	1
CHAPTER 2: METHODS.....	15
CHAPTER 3: RESULTS	23
CHAPTER 4: DISCUSSION	30
CHAPTER 5: CONCLUSIONS	34
REFERENCES.....	35

CHAPTER 1

INTRODUCTION

At its most basic level, attention serves to highlight information in the outside world that is considered important as defined by current task goals. As scientists uncover more details about how the brain perceives and selects visual information, theories of attention grow more complex to reflect the mechanisms of various types of attention and their interactions. Depending on *a priori* knowledge about what information might be relevant, information can be selected based on spatial location, object-based properties or feature-based properties. Although the specific mechanisms of these types of attention are distinct, recent evidence suggests that they are constantly interacting with one another to guide awareness toward behaviorally relevant items (e.g., Sohn et al., 2005; Melcher et al., 2005; Katzner et al., 2009). In particular, this paper explores the close relationship between feature- and object-based attention.

FEATURE-BASED ATTENTION

Feature-based attention refers to the use of a particular feature such as color, orientation or shape to guide visual search. For example, while searching for a pair of red scissors in a drawer full of other office supplies, a feature-based strategy might entail searching for “red things” to locate the scissors. Evidence for this mechanism comes from primate (e.g., Treue & Trujillo, 1999; Bichot et al., 2005), behavioral (e.g., Melcher et al., 2005; Arman & Boynton, 2006) and neuroimaging research (e.g., Saenz et al., 2005; Serences & Boynton, 2007). For instance, Treue & Trujillo (1999) used single-cell

measurements in macaque monkeys to show that features can act as the basis for attention independently of spatial attention. Using moving random dot patterns as stimuli, the authors showed that the neural tuning curves of cells in motion area MT responding to a coherent direction of the dots were enhanced in a multiplicative manner when the monkeys attended to the preferred direction of those cells. Importantly, this attentional enhancement for a stimulus moving in the preferred direction of the cell occurred to the same extent whether the monkeys directed their attention towards a stimulus in the receptive field of the cell or outside the cell's receptive field in the opposite hemifield. In other words, the attentional enhancement was not specific to the attended location. Additionally, when the monkeys attended to a stimulus outside the cell's receptive field that was moving in the opposite direction to the cell's preferred direction, the activity of the cell was suppressed relative to its response to a null-direction stimulus. Together, these results indicate that features (as opposed to a spatial location) can guide behavioral selection (i.e., attention) through gain enhancement of cells' responses to relevant target features and suppression of cells' responses to opposing features. Based on these conclusions, the authors proposed a "feature-similarity gain model" to explain how the similarity between the given response sensitivity of neurons and behaviorally relevant features may drive feature-based attention. Importantly, this model allows for concurrent analysis of features that may not occur within the same receptive field, allowing for a more global, as opposed to spatially specific, attentional bias.

In a similar vein, Bichot et al. (2005) conducted visual search experiments with macaque monkeys to investigate whether parallel mechanisms are responsible for feature-based search based on color and shape. In the first experiment, the monkeys were

instructed to search for an item of a particular color (e.g., red) in an array of colored shapes. The authors measured responses from cells in V4 that either preferentially responded to the target feature (red) or responded to a non-preferred feature (e.g., blue). Additionally, Bichot et al. measured neural responses from cells whose receptive field did not include the current target of spatial attention (when the monkey was looking elsewhere). Importantly, this enabled the investigators to ask whether feature-based attention biased responses in cells that code target information throughout the visual field before target detection occurred. In fact, the authors did find that cells preferentially activated by the target feature showed enhanced activity over cells that preferentially responded to the non-target feature during visual search for the target feature. Interestingly, some cells also showed enhanced response to items that contained a feature that was similar to the target feature; for instance, cells tuned to the color red showed greater response to magenta items during search for a red target versus a blue target. This finding supports the notion that feature-based attention enhances relevant cell activity in a multiplicative manner. In addition, these target-related cells showed increased synchrony with the local field potential (a population of multiple V4 cells firing in synchrony) in the time interval between the end of the current fixation and the median saccade initiation time. This result indicates that feature-based attention may also strengthen postsynaptic responses onto higher level brain regions that guide spatial attention and eye fixations toward the target feature by joining forces among all cells that prefer the target feature. Thus, the authors concluded that such global, parallel mechanisms may allow for speeded search and may help guide spatial attention toward relevant features.

Researchers have also begun to examine whether parallel mechanisms support

feature-based attention in humans. For instance, Arman & Boynton (2006) investigated whether they could modulate the strength of the motion aftereffect (MAE) induced by a task-irrelevant moving dot field as a function of whether the direction of the task-irrelevant stimulus matched a spatially distant, attended dot field (“same” condition) or the task-irrelevant stimulus moved in the opposite direction (“opposite” condition). In the first experiment, subjects performed a speed detection task by attending to one of two dot fields moving upwards or downwards in one hemifield. In the opposite hemifield, a single dot field moving either upwards or downwards was present during the length of the speed detection task. After performing the speed detection task, subjects reported on the length of the MAE induced by the task-irrelevant dot field. The authors found that the strength of the MAE in the task-irrelevant hemifield was enhanced when the stimulus moved in the same versus the opposite direction as the attended dot field, indicating that attentional modulation of the relevant direction had spread throughout the visual field.

Researchers have also investigated the neural mechanisms of feature-based attention in humans using neuroimaging (e.g., Saenz et al., 2002; Serences & Boynton, 2007). For instance, Saenz et al. (2002) used functional magnetic resonance imaging (fMRI) to measure neural responses to a task-irrelevant stimulus that either shared a feature with the attended stimulus or contained a distractor feature. Specifically, subjects were instructed to attend to one of two superimposed moving dot fields that moved in opposite directions (e.g., up and down) in one hemifield. Additionally, a task-irrelevant dot field that moved either in the same or opposite direction as the attended dots was presented in the opposite hemifield. The authors showed that the MT+ response to the task-irrelevant dot field was enhanced when its direction matched the direction of the

attended dots relative to the condition where the task-irrelevant dots moved in the opposite direction as the attended dots. To confirm that this reflected a general feature-based attention effect, Saenz and colleagues also conducted a color feature-based experiment in which subjects attended either red or green stationary dots in one location, while a task-irrelevant dot field in either the attended or ignored color was presented in the opposite hemifield. The authors found similar feature-based results in areas V1-V4, suggesting that this global attention mechanism applies to features other than the direction of motion.

Although the spatial resolution of fMRI is typically not high enough to detect differences in sub-populations of neurons coding specific features (e.g., neurons that are most sensitive to stimuli moving upwards versus downwards), Serences & Boynton (2007) found evidence for global modulation of stimuli moving in specific directions (at 45 versus 135 degrees) using a pattern classification analysis. In this study, subjects attended one of two superimposed moving-dot fields that were moving at 45 or 135 degrees, while an identical, task-irrelevant stimulus was either present or absent in the opposite hemifield. The authors were successful in their attempt to distinguish, using a pattern classifier, whether subjects were attending the 45 degree or 135 degree dot field in the attended location. Importantly, this same classifier was able to detect the currently attended direction in voxels that were spatially selective for the opposite hemifield, indicating that the specific dimension of the target feature (direction of motion) was enhanced in a global fashion.

BASELINE INCREASES

Although the results described above provide compelling evidence for the parallel nature of feature-based attention, one important prediction of the feature-similarity gain model is that feature-based attention increases the baseline firing rate of all neurons preferentially tuned to the target feature. Thus, these cells should show increased response during feature-based attention even in the absence of sensory information across the visual field. Importantly, the classifier implemented by Serences & Boynton (2007) was able to detect the currently attended direction in voxels that were spatially selective for the opposite hemifield, regardless of whether a stimulus was present in this location or not. These results strongly suggest that feature-based attention operates globally, even in regions that do not contain any sensory information. Thus, as the feature-similarity gain model predicts, it appears that feature-based attention automatically biases cells whose feature preferences align with current task goals throughout the visual field, regardless of the presence of sensory information.

OBJECT-BASED ATTENTION

Although independent features such as color, shape and orientation can serve as the units of attention, it is often the case in the visual world that multiple features are bound together within discrete objects. Interestingly, research has shown that attending to a multi-dimensional object necessarily results in automatic processing of all features belonging to that object, even if only one dimension is relevant to the task (e.g., Duncan, 1984; Duncan & Humphreys, 1997; O'Craven et al., 1999). In support of this theory, Duncan (1984) performed a series of experiments showing that subjects were able to judge

two attributes of a briefly presented object as accurately as when reporting one attribute of the object. For instance, subjects could just as easily report both the size of a box and the location of a gap in the box as judging the box's size alone. However, subjects were impaired when they had to report two properties of different objects (e.g., the size of a box and the orientation of a line superimposed on the box), indicating that multiple properties are automatically processed together when they are tied to the same object.

Along these lines, one key prediction of the object-based attention theory is that attending to one feature of an object (e.g., color) will automatically trigger processing of other features inherent in that object (e.g., shape, orientation, motion). This idea was tested by O'Craven and colleagues (1999), who showed that attending to moving faces superimposed over stationary houses not only elicited greater activity in the fusiform face area (FFA) than in the parahippocampal place area (PPA) but also increased activity in the motion-sensitive area MT+ relative to when subjects attended to the stationary houses. This result indicates that attending to one property of an object (i.e., faces) additionally modulates the brain's response to other properties tied to the same object (i.e., motion). Importantly, the movement of the faces was irrelevant to the task in this experiment, supporting the idea that this spreading of attention to other object-bound features occurs in parallel.

More recent theories not only suggest how object-based attention may be achieved in the brain but how these processes may allow for selection of relevant over irrelevant objects in our often cluttered world. For instance, the "integrated competition model" of attention (Duncan & Humphreys, 1997; Duncan, 2006) proposes that visual objects compete with one another such that increased response in cells coding relevant objects is

accompanied by decreased activity in cells coding irrelevant objects. This competition among objects is then integrated across multiple brain regions such that, as one object wins the competition in one system, properties of that object dominate in other brain areas. The result is that all target-related features, including spatial location and any other task-irrelevant properties, are preferentially processed over other non-target features present in the visual field. For example, in the case of the O'Craven and colleagues (1999) experiment, attending to moving faces versus stationary houses resulted in a bias toward face over house processing in the ventral stream, while the faces' motion was prioritized over stationary stimuli in the dorsal stream.

The integrated competition model can also explain why task-irrelevant dimensions of objects are necessarily and automatically processed during object-based attention. Specifically, O'Craven and colleagues (1999) showed that object-based attention results in neural processing of task-irrelevant dimensions tied to the attended object (e.g., irrelevant motion of a moving face activated MT+ during attention to the face). A basic neural model of integrated competition has also been proposed (Duncan & Humphreys, 1997; Duncan, 2006), suggesting that interconnections between different cortical processing regions may support integration of separate features, while feedback connections to earlier visual regions in the brain may both enhance processing of relevant features and suppress those cells coding irrelevant features.

INTERACTIONS OF FEATURE- AND OBJECT-BASED ATTENTION

Although numerous studies have investigated the global aspects of feature-based attention, only a few researchers have begun to explore whether such global mechanisms

may also support object-based attention. Because object-based attention may ultimately act on the various features that comprise a given object (e.g., Duncan & Humphreys, 1997), it is possible that parallel mechanisms are also at work during object-based attention. For example, during a search for red scissors, one might globally activate both cells that prefer the color red and cells that respond best to scissor-like shapes. In support of this notion, Bichot and colleagues (2005) also conducted a conjunction search experiment where monkeys searched for specific colored shapes among an array of distracters that shared either one feature (color or shape) or no features with the target item. Similar to the results found during single-feature search, they found increased activity both in cells that responded to distracters sharing the target color and cells that responded to distracters sharing the target shape.

Additionally, attending to an object may automatically activate all features of the object, not only within the confines of that object's spatial location, as O'Craven and colleagues (1999) demonstrated, but also throughout the visual field. Various recent experiments have demonstrated that this so-called "cross-feature" spreading of attention can occur in spatially distant locations (e.g., Melcher et al., 2005; Sohn et al., 2005; Arman & Boynton, 2006; Katzner et al., 2009). For instance, Melcher and colleagues (2005) tested whether attending to an object in one hemifield would enhance processing of a task-irrelevant stimulus that shared a feature of the attended object in the opposite hemifield. Specifically, subjects attended one of two colored (red or green), superimposed dot fields moving upwards and downwards in one hemifield, while an occasional sub-threshold motion prime (brief, coherent horizontal motion in one color) occurred in the opposite hemifield, which contained flickering red and green dots. Although the subjects were

instructed to detect small luminance changes in the target dot color in the field containing superimposed upwards and downwards moving dots, the authors were interested in the effect of color-based attention on the detection of the spatially distant, task-irrelevant motion prime. Importantly, the motion prime could either contain red or green dots; thus, the color of the motion prime either matched the attended color in the luminance task (e.g., red) or it matched the unattended color (green). In order to measure the degree to which this motion prime was processed, subjects switched their attention to the opposite hemifield after an auditory cue and completed a secondary task that required them to detect whether a second motion probe containing both red and green dots was moving leftwards or rightwards. Since it has been shown that brief coherent motion is more easily detectable when two motion probes are shown sequentially (Melcher & Morrone, 2003), the authors reasoned that performance on the motion discrimination task should reflect the degree of processing of the unattended, sub-threshold probe during the luminance task. In fact, the authors found that presenting the sub-threshold motion prime during the luminance task did enhance performance on the motion discrimination task, but only when the color of the sub-threshold motion prime matched the color attended in the luminance task. In other words, feature-based attention to a particular color enhanced processing of a spatially distant, task-irrelevant motion stimulus that shared the target color.

Interestingly, this result suggests that this global modulation boosted not only the color of the motion stimulus, but also its directional information, since it was the repeated motion that ultimately lead to better motion discrimination. In other words, global feature-based attention also enhanced task-irrelevant features that were spatiotemporally related to the target feature. These results are consistent with the integrated competition hypothesis

(Duncan & Humphreys, 1997; Duncan, 2006), but importantly, they also suggest that integration of relevant and irrelevant features during object-based attention may occur globally, even for objects that are outside the focus of attention.

Additional support for global, cross-feature spreading of attention comes from a study by Sohn and colleagues (2005), who measured both behavioral and fMRI responses to a spatially distant, task-irrelevant motion stimulus during color-based attention. First, the authors measured the strength of the MAE to an unattended dot field in which dots of a single color (red or green) moved coherently; at the same time, subjects attended either red or green randomly flickering dots in the opposite hemifield while performing a luminance task. Despite the fact that motion was neither relevant to the subjects task nor a part of the attended display, Sohn and colleagues found that the unattended, coherent motion stimulus elicited a stronger MAE when its color matched the attended color during the luminance task (“same” condition) versus when it shared the ignored color (“different” condition). Additionally, using fMRI, the authors demonstrated that the neural activity of MT+ in response to the unattended motion stimulus was greater during the “same” versus “different” condition. Together, these results indicate that attention to color spreads to cells coding motion in a global fashion if the moving stimulus shares the attended color.

Although these studies indicate that feature-based attention modulates task-irrelevant features that are spatiotemporally associated with the target feature, they do not necessarily demonstrate whether object-based attention also results in such global modulation of task-irrelevant features. In other words, in the studies described thus far the global aspect of the effects were mediated by the task-relevant feature; that is, subjects attended to the task-relevant feature, this resulted in a global enhancement of that feature,

and when another feature was bound to the attended feature at a task-irrelevant location, it was also enhanced. Another way to describe this is to say that feature-based attention was responsible for the global aspect of the results, and object-based attention at a task irrelevant location was responsible for the enhancement of the irrelevant feature. We asked if the opposite was also possible. Could object-based attention be responsible for some global attention effects? Specifically, attending to an object may automatically activate all features of the object (including task-irrelevant features) not only within the confines of that object's spatial location, as O'Craven and colleagues (1999) demonstrated, but also throughout the visual field. In support of this notion, Arman & Boynton (2006) conducted an experiment similar to their study described above, but subjects now detected luminance changes in either the upwards or downwards moving dot fields. Once again, the task-irrelevant hemifield induced a stronger MAE during the same versus opposite condition, even though subjects did not perform a motion-related task. In other words, the task-relevant feature was luminance, but because the luminance modulated dots that were also moving, the task-irrelevant motion was modulated at a task-irrelevant location.

Additionally, Katzner and colleagues (2009) provided neural evidence for this mechanism by measuring single-cell activity in the MT area of rhesus monkeys in response to a task-irrelevant stimulus. In this study, the monkeys monitored changes in either the direction or color of a moving dot field in one location while ignoring feature changes in a similar stimulus in the opposite visual field (always moving in the cells' preferred direction). Consistent with Arman & Boynton's (2006) findings, the MT response to the task-irrelevant dot field increased when the attended stimulus moved in the same (preferred) versus different (null) direction as the task-irrelevant stimulus, even when the

monkeys were only monitoring the color of the dots in the attended location. Unlike the Melcher and colleagues (2005) and Sohn and colleagues (2005) studies, these results indicate that cross-feature spreading of attention can occur within the attended object and then be applied to task-irrelevant stimuli throughout the visual field. Specifically, Melcher and colleagues and Sohn colleagues found that color-based attention modulated processing of task-irrelevant motion that was spatiotemporally bound to the target color in a spatially distant object. In contrast, Arman & Boynton (2006) and Katzner and colleagues (2009) demonstrated that color-based attention automatically induced processing of the directionality tied to the attended object, which resulted in enhanced processing of that direction throughout the visual field.

CURRENT STUDY

We expanded on the results described above by investigating whether attending to a single feature of a multidimensional object (containing both color and motion) would modulate the neural response to a spatially distant, task-irrelevant object that shared either i) both features (same color and direction), ii) a single feature (either same color/opposite direction or same direction/opposite color), or iii) no features (opposite color/opposite direction) with the attended stimulus. Based on previous work on global feature- and object-based attention, we predicted first that activity should be enhanced at the task-irrelevant location when the stimulus contains the attended feature (color). Second, the irrelevant dimension (motion) bound to the attended color at the attended location should also be enhanced throughout the visual field. Specifically, we expected that early visual cortical areas V1-V4 would elicit the greatest response to the task-irrelevant stimulus location when it shared both features (same color, same direction), an intermediate response when a single feature was present (same color, opposite direction;

opposite color, same direction), and the weakest response to a stimulus containing no shared features (opposite color, opposite direction). Additionally, based on the results of Sohn and colleagues (2005) and Katzner and colleagues (2009), we hypothesized that activity profiles in area MT+ contralateral to the task-irrelevant stimulus would show a similar pattern as early visual cortex, even though the direction of motion was always irrelevant to the task.

CHAPTER 2

METHODS

OBSERVERS

One author (A.L.) and eight naïve subjects (7 males; ages 25-32 years) participated in the experiment. All subjects had normal or corrected-to-normal visual acuity and reported themselves in good health. Each participant gave informed written consent, which was approved by the Institutional Review Board of the University of Illinois at Urbana-Champaign and were paid for participating.

STIMULUS DISPLAY

The stimuli were presented via goggles (Magnetic Resonance Technologies; Willoughby, OH) that were connected to a monitor with a refresh rate of 60 Hz and resolution of 800 x 600. The experiment was programmed using Matlab and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). During stimulus presentation, two square apertures ($9^\circ \times 9^\circ$) appeared 6° to the left and right of and 1° above the center of the screen, at which a gray fixation cross ($0.88^\circ \times 0.88^\circ$) was presented. Each aperture contained 100 dots (radius = 0.08°); the right aperture (attended field) always contained 50 cyan and 50 red dots, while the dots in the left aperture (unattended field) were either all red or all cyan, depending on the condition. In the attended field, 100% of the attended dots (either red or cyan) moved in a coherent direction (either up, down, left or right) for 4 s and then changed direction, rotating through the four possible directions in a random order. The initial direction was chosen randomly, and the order of directions was counterbalanced across all conditions. The ignored dots in the attended field always

moved coherently in an opposing direction from that of the attended dots. The dots in the unattended field either all moved in the same or opposite direction as the attended dots, depending on the condition (Figure 1). All dots in both apertures moved at a rate of $8.77^\circ/s$.

PROCEDURE

At the beginning of each run, subjects were instructed to detect a slight luminance change (dim) in either the red or cyan dots (target color specified prior to each run) in the attended field (right visual field). The target color alternated each run, and the initial target color varied for each subject. Subjects viewed a baseline fixation block (centrally presented gray cross on a black background) for 16 s at the beginning and end of each run as well as in between each experimental block. Subjects were instructed to maintain their gaze on the fixation cross at all times but to attend to the aperture to the right of fixation while ignoring the left aperture. In the attended aperture only, dots in either the target or non-target color dimmed for 500 ms either zero, one or two times (but never simultaneously) within each 16 s block. If two dims occurred within the same block, they either occurred consecutively or were separated by 4 or 8 s intervals. Subjects responded to dims in the target color by pressing a single button on a button box. During each block, the dots in the left, unattended field contained a single color and direction that were related to the target dots in four possible ways (as shown in Figure 1): 1) same color, same direction (SColSDir); 2) same color, opposite direction (SColODir); 3) opposite color, same direction (OColSDir); or 4) opposite color, opposite direction (OColODir). Each of these four conditions appeared three times during each run in a pseudo-randomized order.

There were a total of eight runs, each containing 12 experimental blocks and 13 baseline blocks and lasting 6 minutes and 40 s.

LOCALIZER PROCEDURE

After the eight experimental runs, we also presented two localizer runs in order to extract the most spatially selective voxels responding to the unattended aperture location. Subjects viewed gray moving dots in either the left or right aperture (in the same stimulus locations as the experiment), with the location alternating between the left and right visual fields every block (16 s). The dots moved in a coherent direction at a speed of $8.77^\circ/\text{s}$ for 4 s (up, down, left or right), then rotated through the rest of the possible directions. Each run contained 10 blocks (5 blocks with the left aperture and 5 with the right aperture).

DATA ACQUISITION AND ANALYSIS

Imaging data were acquired in a 3 T head-only scanner (Allegra, Siemens; Malvern, PA) using a standard head coil. For the experimental and localizer runs, we collected echoplanar images (EPs) from the entire brain using a gradient echo sequence [repetition time (TR), 2000 ms; echo time (TE), 20 ms; flip angle, 90° ; image matrix, 64×64 ; field of view, 180×180 mm; slice thickness, 3mm, no gap; voxel size, $2.8 \times 2.8 \times 3$ mm] in 40 ascending transverse slices (between coronal and axial orientations). We collected 200 repetitions for each of the 8 experimental runs and 96 repetitions for each of the two localizer runs. To assist in registering images to anatomical space, we collected high-resolution, T1-weighted SPGR anatomical images (TR, 2000 ms; TE, 2.22 ms; flip angle, 8° ; image matrix, 192×192 ; field of view, 240×240 mm; voxel size, $1.25 \times 1.25 \times 1.25$ mm) in the sagittal plane.

For all participants tested, we also collected multiple high-resolution T1-weighted

anatomical images and EPIs, in a separate session, in response to a standard flickering checkerboard display in order to map retinotopic regions in visual cortex. The functional data from this session were combined with regions of interest (ROIs) from the localizer scan in the previous session and overlaid onto inflated and flattened anatomical images created with Freesurfer software (Fischl et al., 1999). Eye movements were not monitored during the experiment or the retinotopy session.

Data from both the experiment and retinotopy sessions were analyzed using the AFNI software suite (Cox, 1996). The functional data from both the experiment and the localizer were registered, motion-corrected, spike-corrected, smoothed (6 mm FWHM Gaussian blur) and normalized before the regression analysis. In order to test for neural differences among the four main conditions in the unattended stimulus, we constructed four square-wave regressors that corresponded to the time intervals during which each condition appeared during the main experiment. These regressors were then convolved with a gamma function to model the hemodynamic response (time-to-peak = 4.7 s; FWHM = 3.8 s) and submitted to a multiple regression in the framework of the general linear model (GLM). Additionally, we ran a separate GLM for the localizer runs using two convolved regressors that delineated stimulus presentation times in the left and right visual fields.

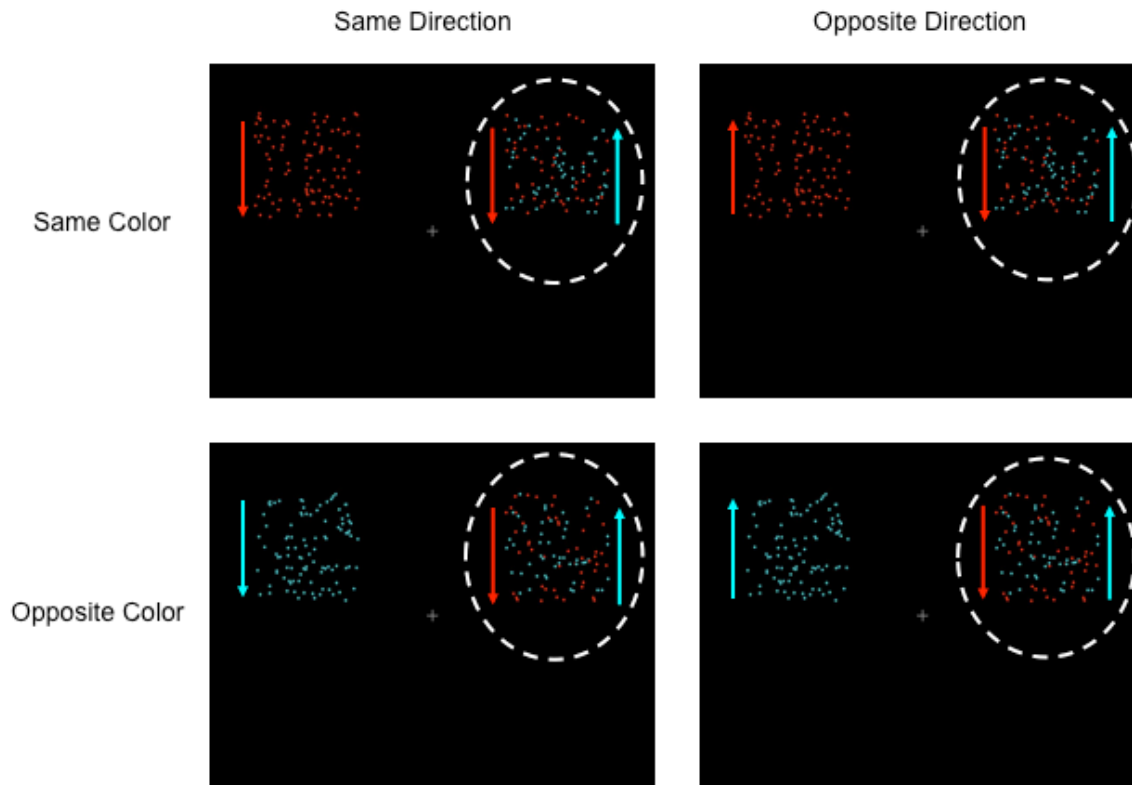
ROI ANALYSIS

ROIs comprising spatially selective voxels for the task-irrelevant location were created by contrasting neural activity responsive to the moving dot field stimulus in the contralateral versus ipsilateral visual field during the localizer. Because the task-irrelevant stimulus always appeared in the left visual field, all ROIs were located in the right

hemisphere. We selected groups of contiguous voxels corresponding to a ventral visual swath (that included V1 through V4), V3a and MT+ using, for each subject, the lowest statistical threshold (i.e. lowest p-value) at which these three regions were spatially separated from one another, resulting in a different threshold for each individual subject that ranged from $p=0.001$ to $p=5.0 \times 10^6$. Although the contrast we used to identify the task-irrelevant location (left visual field stimulus > right visual field stimulus) was chosen to primarily identify voxels contralateral to the task-irrelevant location, there was still some concern that the activity profiles in V3a and MT+ could contain some input from the attended, ipsilateral field, since these regions do not respond exclusively to the contralateral hemifield (e.g., Tootell et al., 1997; Tootell et al., 1998). To check for this possibility, we created a second, more restricted set of V3a and MT+ ROIs, in which the threshold was raised further to isolate the most spatially selective voxels for the contralateral field, such that these restricted ROIs had approximately 50% of the voxels of the original ROIs for each individual (see Table 1 for details). Our logic was the following: if contamination from the ipsilateral (attended) region was driving the effects we saw in the original V3a and MT+ ROIs, then the effects should be weakened when the ROIs are made more spatially selective. Similar or stronger effects in the restricted dorsal ROIs would be taken as evidence that the effects were primarily driven by the contralateral (task-irrelevant) stimulus. For retinotopic mapping, the ventral visual ROIs (expected to be comprised of V1-V4) were combined with the functional map resulting from the retinotopy scan, which contrasted the horizontal versus vertical meridians in the upper and lower visual fields. The resulting activity maps were used to create individual regions V1, V2, VP (V3v in some nomenclatures) and V4 in the right hemisphere. Finally, we applied each ROI

to the regression output of the experimental EPIs for each subject and extracted the beta weights for each task-irrelevant stimulus condition (SColSDir, SColODir, OColSDir and OColODir). These data were then submitted to a within-subjects ANOVA with color (same or opposite), direction (same or opposite) and size (unrestricted versus restricted) as factors.

Figure 1. Example stimulus displays.



Subjects maintained gaze on the central fixation cross while covertly attending (represented by the dashed circle) the right aperture and ignoring the left aperture. Subjects attended either the red or cyan dots, which always moved in opposing directions (e.g., red dots moved downwards while cyan dots moved upwards, schematically shown by colored arrows). Dots in the left, task-irrelevant aperture had either the same or opposite color and direction as the attended dots. Examples display “attend red” conditions with the task-irrelevant stimulus having either the same or opposite color and the same or opposite direction as the attended dots.

Table 1: Restricted voxel analysis.

Subject	MT+ Voxels	MT+ Restricted Voxels	V3a Voxels	V3a Restricted Voxels
S1	49	25	37	19
S2	75	38	182	91
S3	69	35	212	105
S4	50	25	142	71
S5	12	6	94	46
S6	83	42	52	26
S7	14	7	84	42
S8	96	48	109	55
S9	66	33	238	119

CHAPTER 3

RESULTS

Overall average accuracy on the luminance detection task was 82%, ranging from 71-91%, indicating that subjects were sufficiently able to perform the main task. Furthermore, neither accuracy nor false alarm rates on the detection task differed as a function of the color (accuracy, $p=.3$; false alarms, $p=.8$) or the direction (accuracy, $p=.6$; false alarms, $p=1.0$) of the task-irrelevant stimulus, suggesting that subjects' behavior was not significantly influenced by this stimulus. Figure 2 shows percent signal change in V1, V2, VP, V4, V3a and MT+ for each condition in response to the contralateral, task-irrelevant dot field. There was a main effect of color in all regions except MT+ (V1, $p=.01$; V2, $p=.002$; VP, $p=.002$; V4, $p=.003$; V3a, $p=.047$; MT+, $p=.2$), with the task-irrelevant dot field eliciting greater response when the dots' color matched the attended color. Importantly, there was also a main effect of direction in all regions except V2, but even in this area the effect approached significance (V1, $p=.02$; V2, $p=.051$; VP, $p=.02$; V4, $p=.02$; V3a, $p=.008$; MT+, $p=.03$). As shown in Figure 2, the task-irrelevant dot field elicited higher activity when the dots moved in the same direction as the attended dots. Interestingly, there were no interactions between color and direction in any region (V1, $p=.4$; V2, $p=.3$; VP, $p=.2$; V4, $p=.8$; V3a, $p=.2$; MT+, $p=.8$), indicating that these features were modulated independently across the visual field.

Because the receptive fields of some cells in MT+ and V3a include regions of the ipsilateral visual field (e.g., Tootell, 1998), we also performed a restricted voxel analysis for these regions in which a subset of more spatially selected voxels comprised the ROIs (Figure 3; see Methods section for details on this analysis). If the results we saw were due to ipsilateral signals from the attended stimulus then restricting the number of voxels further should reduce the direction effect we observe. Importantly, the main effect of direction was significant in both restricted regions (restricted V3a, $p=.008$; restricted MT+,

$p=.04$). Similar to the results of the unrestricted regions, the color effect was still significant in restricted V3a ($p=.046$) but not in restricted MT+ ($p=.2$). Finally, there were no interactions either between the number of voxels and the effect of color (V3a, $p=.3$; MT+, $p=.7$) or between number of voxels and direction (V3a, $p=.3$; MT+, $p=.8$), indicating that the color and direction effect sizes were comparable for the unrestricted and restricted regions. Importantly, this restricted analysis indicated that the effects from the larger ROIs were not entirely driven by ipsilateral activity.

In order to compare effect sizes for the color and direction variables, we calculated a difference score for the overall color and direction effects in each region (including restricted ROIs for V3a and MT+) using the following formulas:

$$\text{Color Difference Score} = \text{Same color} - \text{Opposite color}$$

$$\text{Direction Difference Score} = \text{Same direction} - \text{Opposite direction}$$

As shown in Figure 4, the sizes of the difference scores were not significantly different for color versus direction effects (V1, $p=.6$; V2, $p=.5$; VP, $p=.5$; V4, $p=.3$; V3a, $p=.9$; MT+, $p=.4$; V3a restricted, $p=.9$; MT+ restricted, $p=.5$), indicating that the task-relevant and task-irrelevant dimensions were modulated to the same extent in the task-irrelevant location.

Figure 2: Neural activation for **a) V1, b) V2, c) VP, d) V4, e) V3a and f) MT+** in the right hemisphere. Bars indicate percent signal change in response to the task-irrelevant aperture for each of the four conditions. Error bars represent ± 1 SEM, calculated for repeated-measures designs (Cousineau, 2005).

Figure 2. A

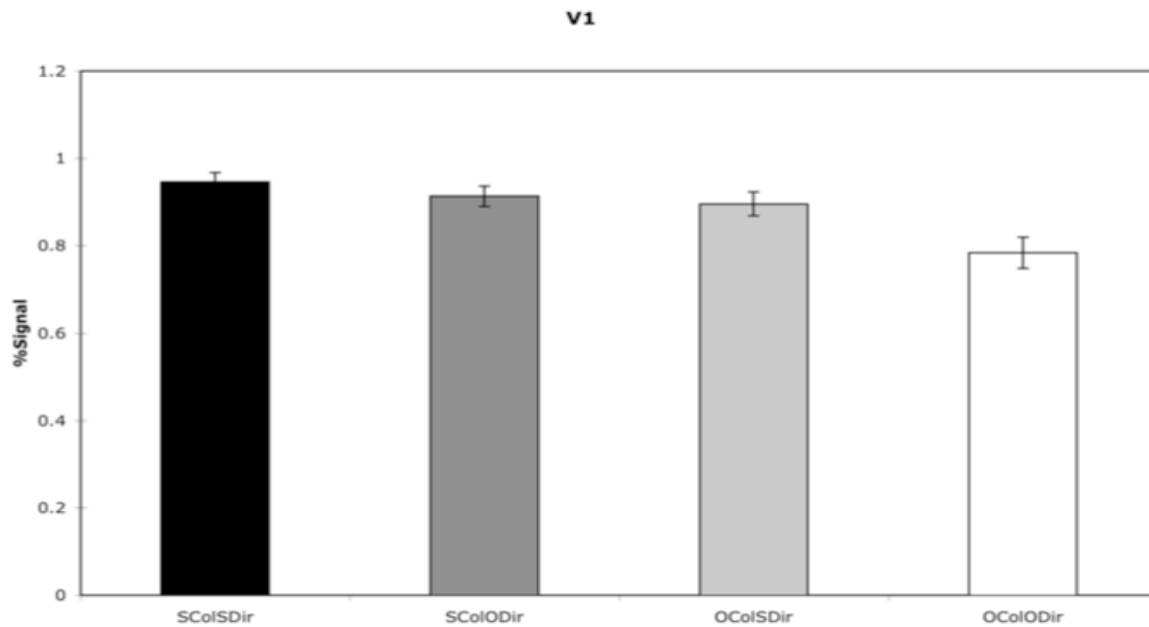


Figure 2. B

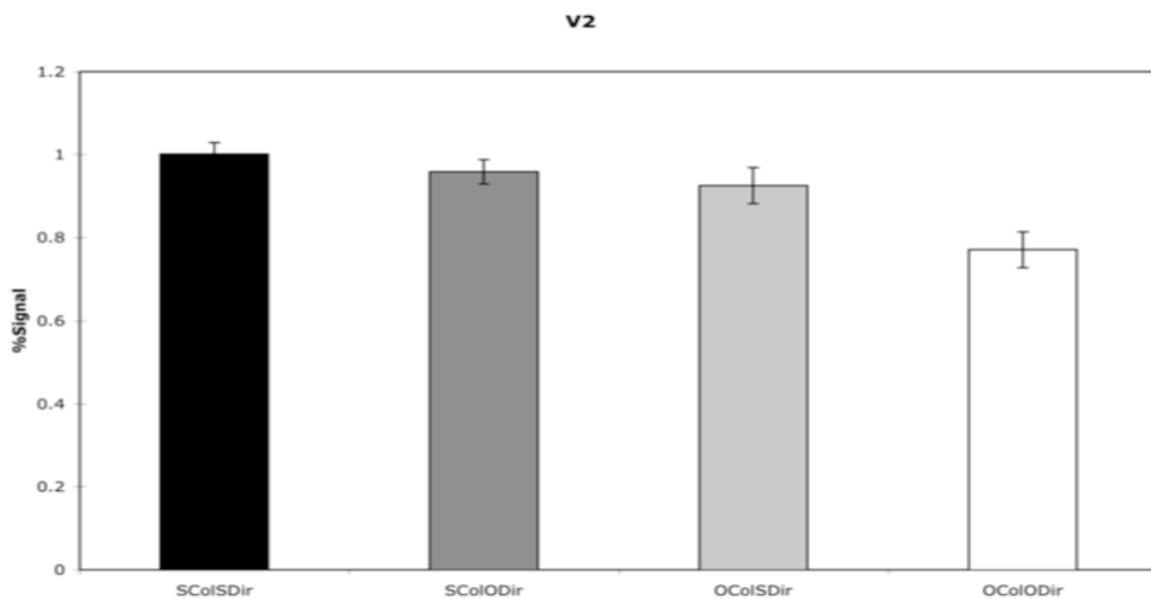


Figure 2. C

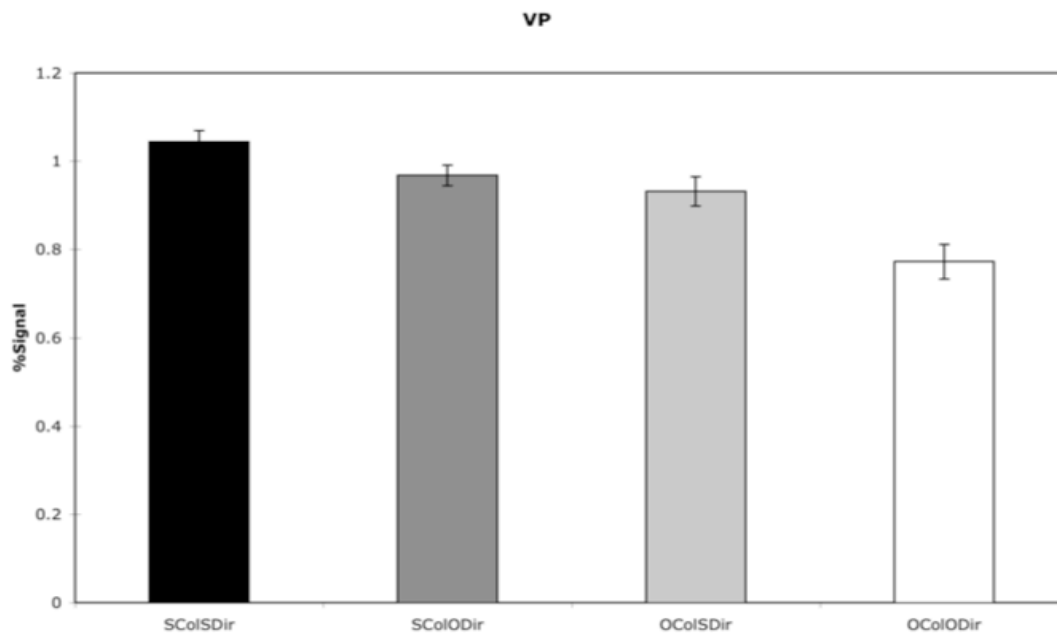


Figure 2. D

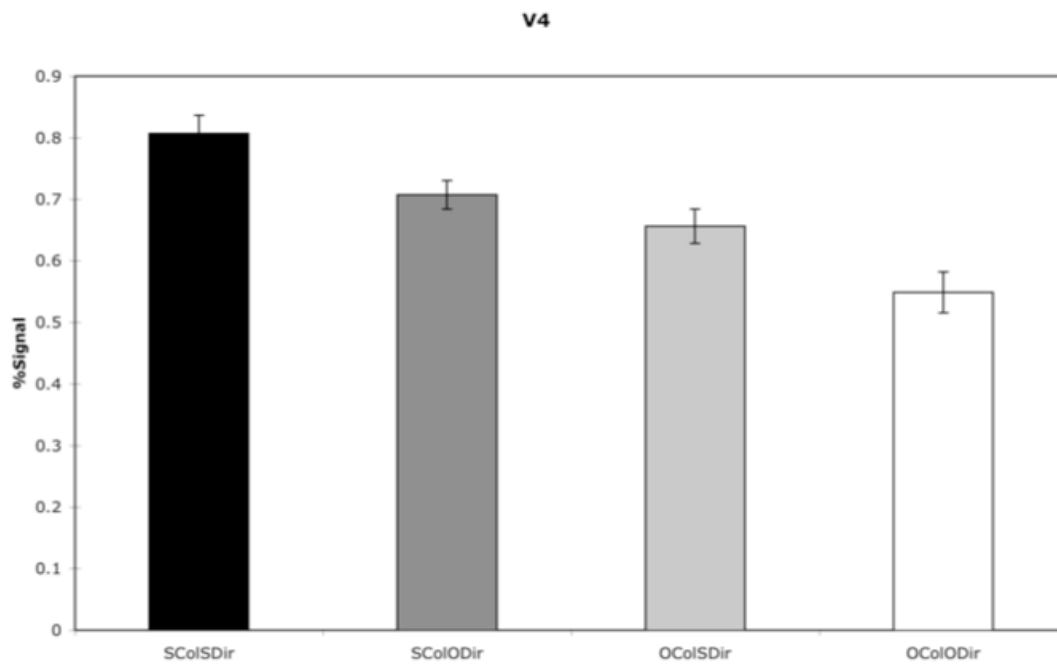


Figure 2. E

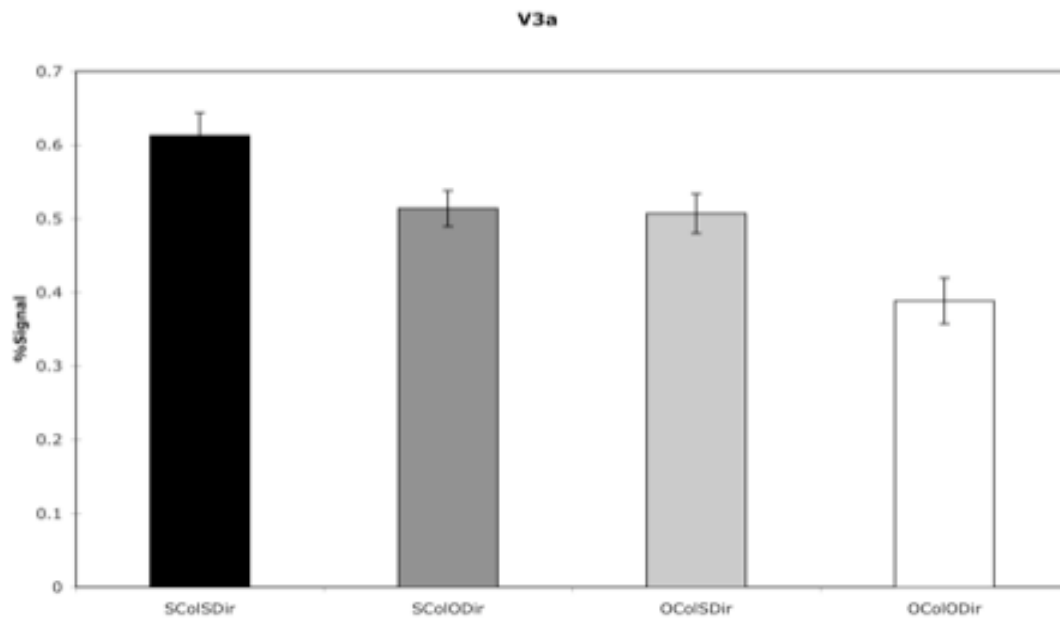


Figure 2. F

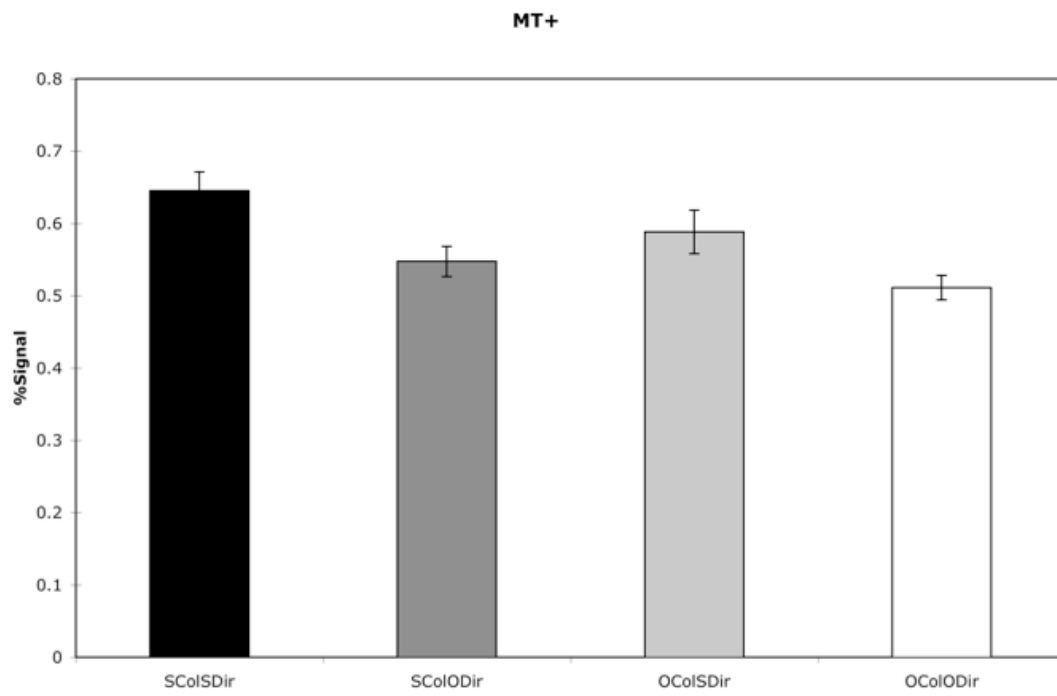


Figure 3: Neural activation for **a) V3a** unrestricted versus restricted and **b) MT+** unrestricted versus restricted (right hemisphere). Bars indicate percent signal change in response to the task-irrelevant aperture for each of the four conditions. Error bars represent ± 1 SEM, calculated for repeated-measures designs (Cousineau, 2005).

Figure 3. A

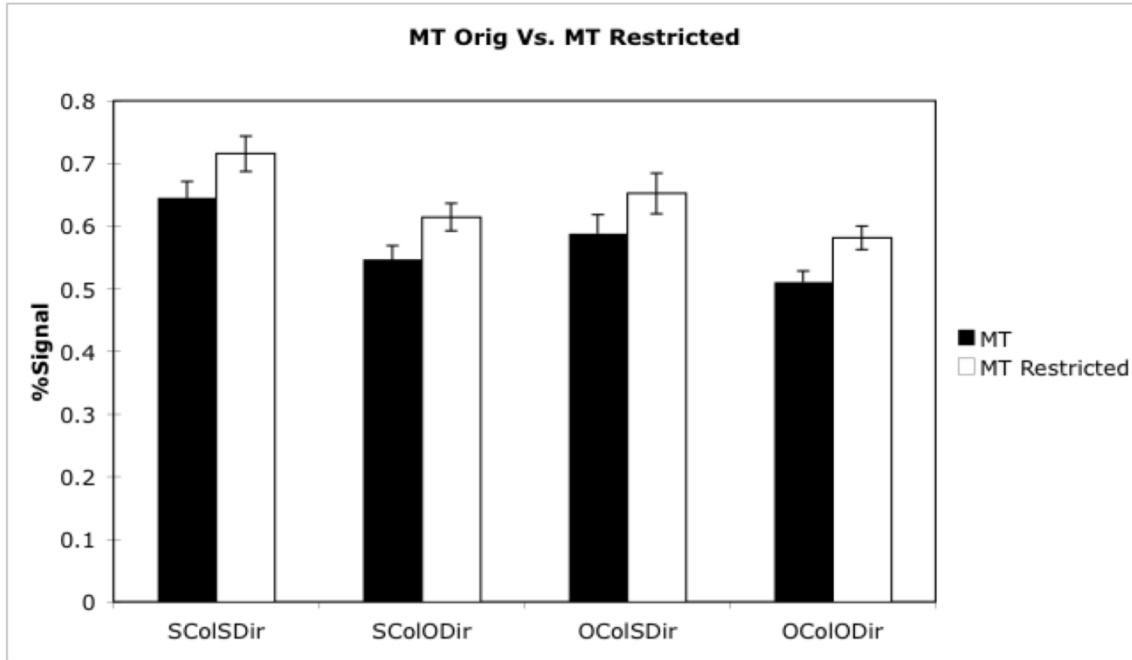


Figure 3. B

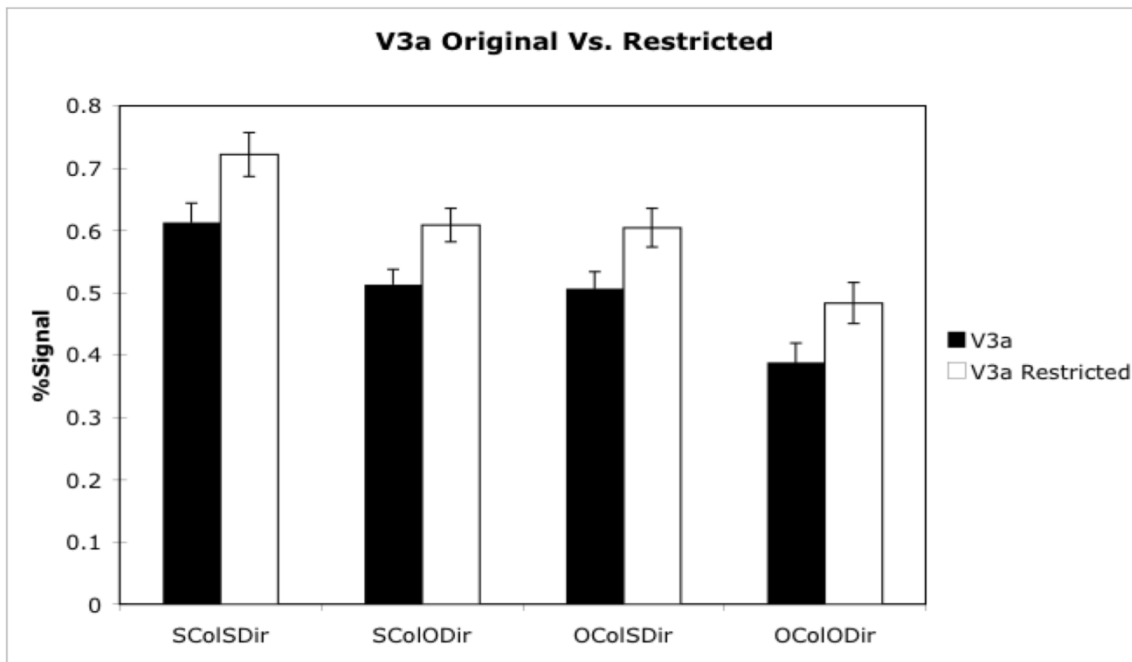
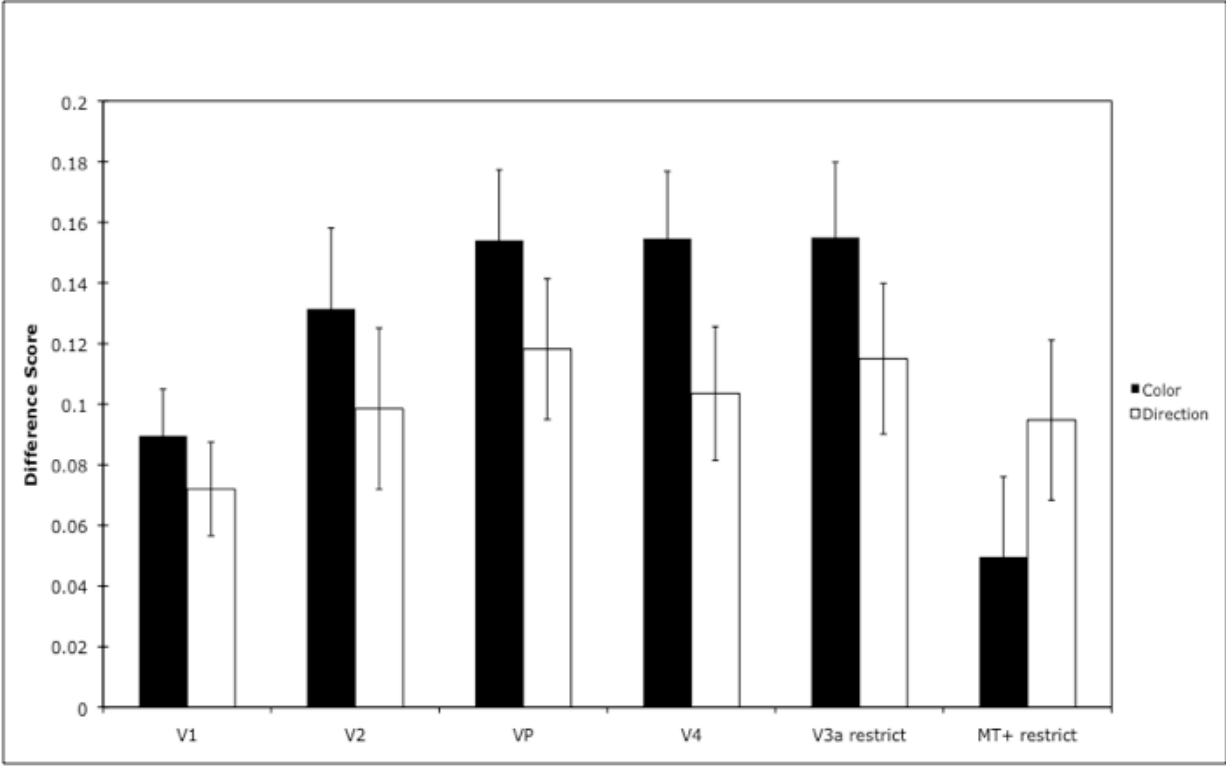


Figure 4: Difference scores for color and direction effects in V1-V4, V3a restricted and MT+ restricted. Color difference score = Same color – Opposite color; direction difference score = Same direction – Opposite direction.



CHAPTER 4

DISCUSSION

Our goal for this study was to determine whether task-relevant (color) and task-irrelevant (motion) properties of an attended object (moving colored dots) would be modulated at a task-irrelevant location. Previous research has shown both that an attended feature (i.e., task-relevant feature) is enhanced throughout the visual field (e.g., Treue & Trujillo, 1999) and that a task-irrelevant feature of an attended object is enhanced at the location of the object (O'Craven et al., 1999). Here we are asking whether the spread of feature attention across the visual field extends to task-irrelevant features that happen to be bound to the task-relevant feature of the attended object. As predicted from previous research, since color was the task-relevant feature for the luminance detection task, we found a significant main effect of color in early visual regions V1 through V4 and V3a responding to the task-irrelevant location, such that the dots in this location elicited greater activity when they matched the color of the attended object (same color conditions; SColSDir and SColODir) than when they matched the color of the ignored object (opposite color conditions; OColSDir and OColODir). In other words, we observed an effect of the attended color at a task-irrelevant location. This result is consistent with previous single-cell (e.g., Treue & Trujillo, 1999) and neuroimaging studies (e.g., Saenz et al. 2002; Serences & Boynton, 2007) that also observed global, enhanced modulation in visual cortex during feature-based attention.

Importantly, even though both motion and the dot field location under investigation were irrelevant to the task, we also found a significant effect of motion direction in early visual regions V1 through V4, V3a and in MT+, with the task-irrelevant dot field eliciting greater response when it was moving in the same direction (SColSDir and OColSdir) versus the opposite direction (SColODir and OColOdir) as the task-relevant dot field. Consistent with prior work in monkeys (e.g., Katzner et al., 2009), this result suggests that attending to

a single object dimension not only leads to enhanced processing of task-irrelevant features tied to that object in the same location (as demonstrated by O'Craven et al., 1999), but also to a task-irrelevant location in the opposite visual field.

Finally, although there were significant main effects of color and direction in ROIs responding to the task-irrelevant location, we did not observe an interaction between color and direction in any region. This lack of an interaction suggests that the task-relevant and task-irrelevant dimensions of the attended object were modulated independently across the visual field. If it were the case that only bound features of the attended object were enhanced at the task-irrelevant location, then we would have observed modulation there only when the color of the task-irrelevant stimulus matched the attended color (i.e. during SColSDir and SColOppDir conditions). However, we also observed enhanced activity to the task-irrelevant stimulus when the direction but not the color was the same as the attended dot field (i.e., during OColSDir). Importantly, this further supports the idea that the global effect of the task-irrelevant dimension was due to feature-based versus object-based attentional mechanisms.

Our findings raise several important questions: first, why should the visual system care about the presence of such task-irrelevant features, especially if they appear in task-irrelevant locations? Consistent with the integrated competition hypothesis (Duncan & Humphreys, 1997; Duncan, 2006), one possibility is that this is simply a consequence of how the visual system is built to deal with attended objects. In the context of the current study, such a model could explain how various visual areas were modulated by motion direction in a global fashion despite the fact that motion was task-irrelevant. By virtue of attending to the color of the relevant dot field as a whole, subjects may have automatically coded the direction of motion associated with the attended dots. Once this motion direction was selected, albeit indirectly, the modulation spread throughout the visual field,

since such feature-based selection is ultimately a global mechanism (e.g., Treue & Trujillo, 1999).

A second issue concerns the source of this global, task-irrelevant modulation. Presumably, initially top-down signals from fronto-parietal cortex serve to boost the attended color in ventral visual cortex. How then does this enhancement spread to a motion direction? In predicting that the direction of the attended dots would be modulated in the task-irrelevant location, one might have expected that this effect would be primarily observed in dorsal regions more typically associated with coding direction of motion, such as MT+ and V3a. In fact, we did find significant main effects of direction in these regions, but we also found comparable effects in ventral regions V1 through V4, which are more commonly associated with processing properties necessary for object recognition such as color, form and orientation (e.g., Mishkin & Ungerleider, 1982). However, the ventral motion effect is not entirely surprising given that numerous studies have shown that the parvocellular pathway, which predominantly codes color and form information, and the magnocellular pathway, which is more sensitive to contrast and motion information (e.g., Ferrera et al., 1992) are not completely restricted to the ventral and dorsal streams, respectively. For example, Gegenfurtner et al. (1996) showed that both distinct and common cell populations in macaque V2 preferentially respond to multiple features, such as color and direction of motion. Additionally, Ferrera et al. (1992) observed that macaque area V4 receives both parvocellular and magnocellular inputs. Finally, Huk et al. (2001) demonstrated that areas V1, V2, VP and V4 are also direction selective in humans using an adaptation paradigm with fMRI. Thus, it is possible that the enhancement of color sensitive cells spread to motion sensitive cells within the early ventral regions themselves, either by virtue of the same cells coding both color and motion (e.g. Gegenfurtner et al., 1994) or via lateral connections between cells that code different properties (Gegenfurtner et al., 1996).

An alternative possibility is that the early ventral visual areas received information

about motion direction indirectly via feedback from more dorsal regions such as V3a and MT+ (e.g. Duncan, 2006). In other words, the enhancement observed in the ventral visual areas may not be mediated by direction-sensitive cells in these regions, but result from some interaction between the ventral and dorsal streams as a result of some binding process. This idea is supported by two findings: first, reciprocal anatomical connections between V1 through V4 and V3a and MT have been found in primate visual cortex (e.g., Felleman & Van Essen, 1991). Second, as shown in Figure 4, the size of the direction difference score increased from V1 to V4, consistent with recent evidence that attentional feedback progresses from higher to lower visual areas (Buffalo et al., 2009); however, this linear trend was not significant ($p=.4$). Additionally, because there are only a limited number of direction-selective cells in V4 (e.g., Felleman & Van Essen, 1987), this finding also suggests that the direction effect in V4 may be due to connections to dorsal regions.

Another unresolved issue is whether all task-irrelevant properties of attended objects are affected equally or if certain dimensions (e.g., color, orientation, direction of motion) are prioritized over others. For instance, if subjects in our study had instead attended to the direction of the dots and ignored the color, would the global effects of color be comparable to the direction effects reported in the current study? Finally, an important question that deserves further inquiry is whether there are any behavioral consequences to such global object-based effects; for instance, does the neural modulation translate to increased perceptual sensitivity? If so, such a mechanism could aid in visual search by highlighting locations containing items that share features with the target item.

CHAPTER 5

CONCLUSIONS

Although further work is necessary to uncover the specific neural circuitry involved and what, if any, effect it may have on behavior, our results indicate that object-based attention ultimately manifests as a feature-based attention mechanism that enhances all properties of the attended object throughout the visual field, regardless of whether these properties are relevant to the task. Although serial attention may be necessary for initially integrating multiple dimensions of an object, such as color and motion (e.g., Treisman & Gelade, 1980), it also appears that, once selected, these dimensions can become “unbound” and modulated separately in parallel.

REFERENCES

- Arman, A.C., Ciaramataro, V.M., & Boynton, G.M. (2006). Effects of feature-based attention on the motion aftereffect at remote locations. *Vision Research*, *46*, 2968-2976.
- Bichot, N.P., Rossi, A.F., & Desimone, R. (2005). Parallel and serial neural mechanisms for visual search in macaque area V4. *Science*, *308*, 529-534.
- Brainard, D. H. (1997). The Psychophysics Toolbox, *Spatial Vision* *10*:433-436.
- Buffalo, E.A., Fries, P., Landman, R., Liang, H., Desimone, R. (2010). A backward progression of attentional effects in the ventral stream. *Proceedings of the National Academy of Sciences*, *107*, 361-365.
- Cox, R.W. (1996). AFNI: software for analysis and visualization of functional magnetic resonance neuroimages. *Computational Biomedical Research*, *29*, 162-173.
- Duncan, J., Humphreys, G. & Ward, R. (1997). Competitive brain activity in visual attention. *Current Opinion in Neurobiology*, *7*, 255-261.
- Duncan, J. (2006). Brain mechanisms of attention. *Quarterly Journal of Experimental Psychology*, *59* (1), 2-27.
- Felleman, D.J. & Van Essen, D.C. (1987). Receptive field properties of neurons in area V3 of Macaque monkey extrastriate cortex. *Journal of Neurophysiology*, *57*(4), 889-920.
- Ferrera, V.P., Nealey, T.A., & Maunsell, J.H.R. (1992). Mixed parvocellular and magnocellular geniculate signals in visual area V4. *Nature*, *358*, 756-758.
- Fischl, B., Sereno, M.I., Dale, A.M. (1999). Cortical surface-based analysis. II: Inflation, flattening, and a surface-based coordinate system. *Neuroimage*, *9*, 195-207.
- Gegenfurtner, K. R., Kiper, D. C., Beusmans, J., Carandini, M., Zaidi, Q. & Movshon, J. A. (1994). Chromatic properties of neurons in Macaque MT. *Visual Neuroscience*, *11*, 455-466.
- Gegenfurtner, K.R., Kiper, D.C. & Fenstemaker, S.B. (1996). Processing of color, form and motion in macaque area V2. *Visual Neuroscience*, *13*, 161-172.
- Huk, A.C., Ress, D. & Heeger, D.J. (2001). Neuronal basis of the motion aftereffect reconsidered. *Neuron*, *32*, 161-172.
- Katzner, S., Busse, L., & Treue, S. (2009). Attention to the color of a moving stimulus modulates motion-signal processing in macaque area MT: evidence for a unified attentional system. *Frontiers in Systems Neuroscience*, *3*(12), 1-8.
- Melcher, D., & Morrone, M.C. (2003). Spatiotopic temporal integration of visual motion across saccadic eye movements. *Nature Neuroscience*, *6*, 877-881.
- Melcher, D., Papanicolaou, T.V., & Vidnyánszky, Z. (2005). Implicit attentional selection of visually bound features. *Neuron*, *46*, 723-729.
- O'Craven, K.M., Downing, P.E. & Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature*, *401*, 584-587.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies, *Spatial Vision* *10*:437-442.
- Saenz, M., Buracas, G.T. & Boynton, G.M. (2005). Global effects of feature-based attention in human visual cortex. *Nature Neuroscience*, *5*(7), 631-632.
- Serences, J.T. & Boynton, G.M. (2007). Feature-based attentional modulations in the absence of direct visual stimulation. *Neuron*, *55*, 301-312.
- Sohn, W., Chong, S.C., Papanicolaou, T.V., Vidnyánszky, Z. (2005). Cross-feature spread of

- global attentional modulation in human area MT+. *Neuroreport*, 16(12), 1389-1393.
- Treisman, A.M. & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, 12, 97-136.
- Treue, S. & Martinez-Trujillo, J.C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature*, 399, 575-579.
- Ungerleider, L. G. and M. Mishkin (1982). Two cortical visual systems. In D.J.Ingle, M.A.Goodale, and R.J.W.Mansfield (Eds.), *Analysis of Visual Behavior*, pp. 549--586. Cambridge, MA: MIT Press.