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Global feature-based attention for motion and color

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Abstract

We used a divided attention psychophysical task to test the hypothesis that visual attention to a stimulus feature[1] facilitates the processing of other stimuli sharing the same feature. Performance on a dual-task was significantly better when human observers divided attention across two spatially separate stimuli sharing a common feature (same direction of motion or same color) compared to opposing features. This attentional effect was dependent upon the presence of competing stimuli. These results are consistent with a spatially global feature-based mechanism of attention that increases the response of cortical neurons tuned to an attended feature throughout the visual field.

Keywords: Feature-based attention; Dual-task; Divided attention; Psychophysics; Human

1. Introduction

The content of our visual experience largely depends on our ability to distribute selective attention throughout the visual field. Some early theories compared the distribution of visual attention to a "spotlight" enhancing the processing of stimuli located within the spatial focus of attention (Eriksen & St James, 1986; Posner & Snyder, 1980). More recent theories propose that visual attention enhances the activity of cortical neurons that encode behaviorally relevant stimulus properties including, not only spatial location, but also features and object identity (Desimone & Duncan, 1995; Duncan et al., 1997; Treue & Martinez Trujillo, 1999). For example, these models predict that when an observer searches for an object of a particular color, attention sensitizes neurons with receptive field locations throughout visual space that respond to that color. Recent electrophysiological studies in monkeys provide evidence for attentional selection based on non-spatial stimulus properties. Chelazzi and colleagues reported that searching for a stimulus enhanced baseline activity in inferior-temporal cortical neurons preferring that stimulus, even prior to stimulus presentation (Chelazzi et al., 1993, 1998). In addition, Treue and Martinez Trujillo showed that attention to a particular direction of motion increased the stimulus-evoked response of MT neurons tuned to that direction of motion with receptive fields outside the attended location (Treue & Martinez Trujillo, 1999).

In a recent study, we used fMRI to study feature-specific attentional effects in human visual cortex (Sàenz et al., 2002). Observers were presented with two stimuli, one to attend and one to ignore, placed to the left and right of a central fixation point. The attended stimulus was a circular aperture of two transparently overlapping fields of upward and downward moving dots, and the ignored stimulus was a circular aperture of a single field of dots moving in either direction, up or down. On the attended side, subjects performed a speed discrimination task alternately on the upward and downward moving fields of dots. Because the fields of dots on the attended side were overlapping, either direction of motion could be attended without changing the stimulus or the spatial distribution of attention. We found that the fMRI

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[1] We define a 'feature' as a property within a stimulus dimension. For example, upward and downward directions of motion are two opposing features within the stimulus dimension of motion, and red and green are opposing features within the stimulus dimension of color.

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response to the unchanging, ignored stimulus in the opposite visual hemifield was increased when observers attended the matching direction of motion compared to the opposing direction of motion. This feature-specific attentional modulation was observed in multiple human visual areas representing the earliest stages of cortical visual processing (V1, V2, V3, V3A, and V5/MT+). Similar results were obtained in a second experiment using color as the attended feature. These findings suggest that feature-specific attention enhances the processing of stimuli that have behaviorally relevant features throughout the visual field.

Feature-specific attention may thus profoundly impact our ability to process multiple stimuli in a complex visual scene. Specifically, if attention to a stimulus feature enhances the processing of other stimuli with that same feature, this should facilitate the distribution of attention across multiple stimuli with common features compared to opposing features. The aim of the present study was to test that prediction. We employed a dual-task psychophysical experiment that required subjects to make concurrent discrimination judgments on two spatially separate stimuli containing either the same feature (the same direction of motion or the same color) or opposing features (opposing directions of motion or opposing colors). We predicted that attending to stimuli with common features would facilitate their concurrent processing.

We adapted the stimuli from our previous fMRI experiment in order to relate the results as best as possible. Observers were instructed to divide attention equally across two stimuli placed to the left and right of a central fixation point. In the first experiment, each stimulus was a circular patch consisting of two transparently overlapping fields of upward and downward moving dots (Fig. 1a). Subjects concurrently performed a speed discrimination task on one field of dots from each side, either moving in the same direction (up or down on both sides) or in different directions (up on one side and down on the other). Thus, without changing the visual display or the spatial distribution of attention, subjects divided attention across stimuli composed of either a common feature or opposing features. In a second experiment, we adapted the stimulus to use color as the attended feature. Stimuli were composed of transparently overlapping fields of red and green stationary dots (Fig. 2a). Subjects simultaneously performed a luminance discrimination task on one field of dots from each side. In both experiments, subjects performed significantly better on the dual-task when dividing attention between two fields of dots with the same feature (same direction of motion or same color) rather than opposing features (opposing direction of motion or opposing color). Furthermore, these attentional effects were reduced in additional experiments that eliminated the need to filter out distracting stimuli.

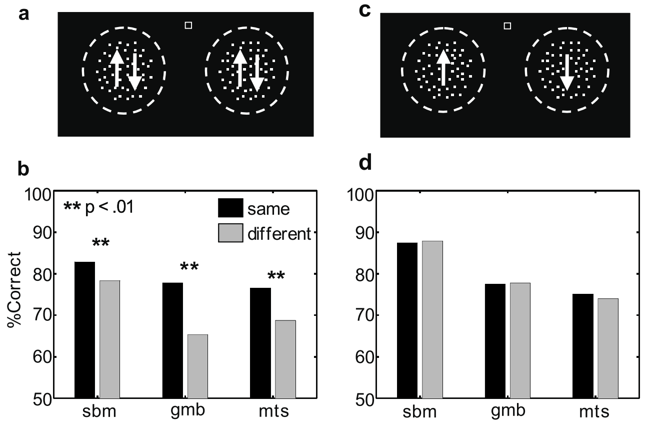

Fig. 1. (a) Stimulus diagram of the direction of motion experiment. Both left and right stimuli were composed of overlapping fields of upward and downward moving dots. While fixating, subjects concurrently performed a speed discrimination task on one field of dots from each side, either moving in the same direction (up or down on both sides) or in different directions (up on one side and down on the other). (b) Task performance was better when dividing attention across *same* vs. *different* directions for all subjects. (c) Stimulus diagram of the same experiment without distractors. Left and right stimuli were each composed of a single field of moving dots. Subjects concurrently performed a speed discrimination task on the single field of dots from each side, either moving in the same or different directions (only one example is diagrammed here). (d) The difference in task performance when dividing attention across *same* vs. *different* directions was reduced for all subjects.

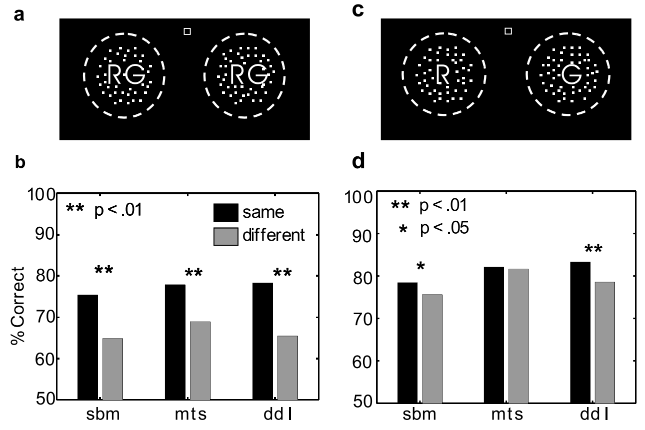

Fig. 2. (a) Stimulus diagram of the color experiment. Both left and right stimuli were composed of overlapping fields of red and green stationary dots. While fixating, subjects concurrently performed a luminance discrimination task on one field of dots from each side, either of the same color (red or green on both sides) or of different colors (red on one side and green on the other). (b) Task performance was better when dividing attention across *same* vs. *different* colors for all subjects. (c) Stimulus diagram of the same experiment without distractors. Left and right stimuli were each composed of a single field of colored dots. Subjects concurrently performed a luminance discrimination task on the single field of dots from each side, either of the same color or of different colors (only one example is diagrammed here). (d) The difference in task performance when dividing attention across *same* vs. *different* colors was reduced for all subjects.

2. Methods

2.1. Direction of motion experiment

The stimulus was composed of two spatially separate circular apertures (radius 5 deg) of moving random dots centered 11 deg to the left and right of and 2.5 deg below a central fixation point (Fig. 1a). Dots were white (560 cd/m^2) on a gray background (230 cd/m^2) and were each 0.6 deg of visual angle in width. The left and right sides of the display were identical and were each composed of two overlapping fields of upward and downward moving dots (50 dots per field). The dots within each field moved coherently and had limited lifetimes (200 ms) to prevent the tracking of individual dots. Because of their opposing motions, the overlapping fields of upward and downward moving dots on each side perceptually segregated allowing observers to selectively attend to a single direction of motion on each side. To direct their attention, subjects were instructed to perform a threshold level speed discrimination task on one field of dots from each side at the same time (dual-task). This was designed so that subjects could perform the dual-task on one field of dots from each side moving in either the same direction (both up or both down) or in different directions (one up and one down) without changing the visual stimulus, eye position, or the spatial distribution of attention.

The dual-task was performed in successive two-interval forced choice trials (2-IFC) initiating every 3.3 s. During each trial, the stimulus was presented for two sequential 500 ms intervals separated by a 100 ms interval in which only the fixation point was present. Brief presentations of 500 ms were used to encourage subjects to perform the left and right discriminations simultaneously rather than sequentially. For each of the four fields of dots, a threshold level speed change occurred between the two intervals on 50% of trials. Specifically, on 50% of the trials, the dots moved at the baseline speed during one interval and at a slightly incremented speed during the other interval (in either order). On the other 50% of trials, there was no speed change across intervals; the dots moved at the baseline speed during both intervals. Whether a speed change occurred or not was independently randomized for each of the four fields of dots on every trial. At the end of each trial, the subjects' task was to report whether or not a speed change occurred within each of the two attended fields of dots (and speed changes that occurred in the distracting field of dots were to be ignored). Thus, there were four equally probable responses: change (on left)/change (on right), change/no change, no change/change, or no change/no change. Subjects indicated these responses by pressing 1 and 0 on a keypad in the following combinations: 11, 10, 01, and 00, respectively. Feedback was given during the inter-trial interval as a small 'yes' or 'no' appearing above the fixation point corresponding to each side.

It is important to note that the task was not to compare speeds across sides but rather to make an independent judgment on each side. On every trial, baseline speeds were different on each side so that observers could gain no benefit from comparing stimulus speeds across sides. If the baseline speed for the two fields of dots on the left was 10 deg/s, then the baseline speed for the two fields of dots on the right was 20 deg/s, and vice versa. Whether the higher baseline speed occurred on the left or right side was randomly determined for each trial. The difference in baseline speeds across sides was essential, as it would be a trivial result if subjects performed better when judging two fields of dots moving in the same direction because they benefited from comparing speeds across sides.

There were four combinations of dot fields which could be attended per trial: up (on left)/up (on right), down/down, up/down, and down/up. Data were collected in blocks of 36 trials of each of the four trial types. At the start of a block of trials, a phrase presented on the screen instructed subjects which combination of dots to attend for that block (e.g. "Attend Up on the Left and Down on the Right"). Subjects each performed nine interleaved blocks of each of the four trial types yielding a total of 1296 trials per subject.

Three subjects participated in this experiment. MTS and GMB were authors and SBM was a paid volunteer. Subjects (ages 25–36) had normal or corrected-to-normal visual acuity. All subjects gave written, informed consent. Before data collection, subjects trained equally on all four trial types until stable performance was achieved (minimum 1000 practice trials). Speed increments were chosen that resulted in a performance of ≈80% correct on the dual-task. The speed increments used for all subjects were 7.1 deg/s for dots with a baseline speed of 10 deg/s and 9.6 deg/s for dots with a baseline speed of 20 deg/s.

2.2. Direction of motion experiment without distractors

The same three subjects (MTS, GMB, and SBM) participated in a second version of this divided attention experiment that eliminated the need to filter out distracting motion. In this second experiment, only a single field of moving dots was presented on each side of the fixation point (Fig. 1b). Subjects performed the same speed discrimination dual-task as in the previous experiment on dots moving in either the same or in different directions of motion. Note that with only a single field of dots presented on each side, the stimulus was physically different during each of the four conditions: up (on left)/up (on right), down/down, up/down, and down/up. Subjects again performed nine interleaved blocks of 36 trials of each of the four trial types, yielding a total of 1296 trials per subject. Without distractors, the task was less difficult and speed increments were reduced to maintain performance at ≈80% correct. The speed increments used for all subjects were 5.7 deg/s for dots with a baseline speed of 10 deg/s and 7.9 deg/s for dots with a baseline speed of 20 deg/s.

Performing the dual-task both with and without distractors allowed us to compare our results to previous studies reporting greater effects of attention when multiple stimuli compete for attentional selection within single neuronal receptive fields (Luck et al., 1997; Moran & Desimone, 1985; Motter, 1993; Treue & Martinez Trujillo, 1999; Treue & Maunsell, 1999). If a performance difference between trial types found in the first experiment was due to attention, then we might expect the effect to be diminished by removing the overlapping distracting dots. Alternatively, if the performance difference was simply due to benefit gained from comparing speeds across sides, then we would expect that benefit to remain after removing the distractors.

2.3. Color experiment

We performed an analogous second experiment using color as the attended feature. The general methods were the same as in the first experiment and only the differences are emphasized here. The left and right sides of the display were each composed of two overlapping fields of stationary red and green random dots (50 dots per field) (Fig. 2a). Whenever there were overlapping pixels between two dots in the display, those pixels were randomly assigned the color of one of the two overlapping dots so that neither field of dots appeared to be in front of the other. Stimuli were displayed in the upper visual hemifield (2.5 deg above fixation) to be consistent with our fMRI experiment involving feature-based attention to color. The dots had limited lifetimes (200 ms) and appeared to flicker. Subjects were instructed to perform a threshold level luminance discrimination task on one field of dots from each side at the same time. Under identical stimulus conditions, attention could thus be divided across two fields of dots with either the same color (both red or both green) or with different colors (one red and one green).

During each 2-IFC trial, the task was to report whether or not a threshold level luminance change occurred between the two intervals for each of the two attended fields of dots. As in the first experiment, whether a luminance change occurred or not was independently randomized for each of the four fields of dots on every trial. There were four equally probable responses: change (on left)/change (on right), change/no change, no change/change, or no change/no change. Furthermore, baseline luminances on the two sides were randomized across trials so that subjects could not benefit from comparing luminances across sides.

There were four combinations of dot fields which could be attended: red (on left)/red (on right), green/green, red/green, and green/red. Data were collected in blocks of 36 trials of each of the four trial types. Subjects each performed nine interleaved blocks of each of the four trial types, yielding a total of 1296 trials per subject.

Subject MTS was an author and SBM and DDL were paid volunteers. Subjects (ages 25–27) had normal visual acuity and color vision. All subjects gave written, informed consent. Before data collection, subjects trained equally on all trial types until stable performance was achieved (minimum 1000 practice trials). Luminance increments were chosen that resulted in performance of ≈80% correct on the dual-task. The red and green dots were not equated for luminance so each had different baseline luminance values. Luminance increments used for all subjects were 15 and 17 cd/m^2 for red dots with baseline luminances of 137 and 153 cd/m^2, respectively. Luminance increments were 25 and 28 cd/m^2 for green dots with baseline luminances of 225 and 250 cd/m^2, respectively (Weber fractions of 0.11).

2.4. Color experiment without distractors

The same three subjects (MTS, SBM, and DDL) performed a second version of the color experiment that eliminated the need to filter out distracting stimuli. Only a single field of dots was presented on each side of the fixation point (Fig. 2b). The fields were either of the same color or of different colors: red (on left)/red (on right), green/green, red/green, or green/red. Data was collected in interleaved blocks of 36 trials of each of the four trial types, yielding a total of 1296 trials per subject. Surprisingly, the dual-task was not noticeably easier without distractors and the same luminance increment thresholds were used as in the previous color experiment to maintain a task performance of ≈80%.

2.5. Equipment and stimulus details

Stimuli for both experiments were generated on a Macintosh PowerBook computer using Matlab v4.3 and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Stimuli were displayed using an LCD projector (60 Hz frame rate) using a back-projection screen. Subjects sat in a darkened room in an upright position with their head in a chin-rest and viewed the screen at a distance of 18 cm. Stimuli were presented using an LCD projector instead of a CRT monitor in order to match the stimulus characteristics used in the previous fMRI experiment (Sàenz et al., 2002).

3. Results

3.1. Direction of motion experiment

Subjects performed the dual-task on two fields of dots moving in either the same direction (*same* trials) or different directions (*different* trials). The visual display was unchanged across *same* and *different* trials; only the attentional state of the observer differed. Fig. 1a plots performance on *same* trials compared to *different* trials for each of three subjects. All subjects performed significantly better on *same* trials than on *different* trials (SBM, 82.9% vs. 78.3% correct; GMB, 78.8% vs. 65.4%; MTS, 76.6% vs. 68.8%; $p < 0.01$ for each subject; $n = 1296$ trials/subject). Subjectively, subjects reported that attending to a particular direction of motion on one side seemed to make the dots moving in the same direction on the other side more salient, thereby facilitating task performance on same trials and interfering with task performance on different trials.

3.2. Direction of motion experiment without distractors

Subjects performed the dual-task in the absence of distracting stimuli. As shown in Fig. 1b, there was no difference in performance on *same* vs. *different* trials for all subjects (SBM, 87.4% vs. 87.9% correct; GMB, 77.5% vs. 77.8%; MTS, 75.1% vs. 74.0%, $p > 0.05$ for each subject; $n = 1296$ trials/subject).

3.3. Short presentation trials

It could be argued that the 500 ms presentation intervals were not sufficiently short to guarantee simultaneous performance of the dual-task. To address this concern, we reran the full experiment for one subject with 200 ms presentation intervals. Additional training was required for that subject to perform the dual-task with shorter presentation intervals. The speed increments used were 9.0 deg/s for dots with a baseline speed of 10 deg/s and 9.6 deg/s for dots with a baseline speed of 20 deg/s. With the shorter presentation times, performance on same trials remained near 80% correct while performance on different trials dropped to near chance (MTS, 80.1% vs. 59.6%; $p < 0.001$). As with the 500 ms presentations, there was no statistical difference in performance across the same and different conditions when the distracting fields were removed (MTS, 79.6% vs. 77.5%, $p > 0.05$).

3.4. Color experiment

Subjects performed the dual-task on two fields of dots of either the same color (*same* trials) or different colors (*different* trials). Again, the visual display was unchanged across *same* and *different* trials; only the attentional state of the observer differed. Fig. 2a plots performance on *same* trials compared to *different* trials for each of three subjects. Consistent with the direction of motion experiment, all subjects performed significantly better on *same* trials compared to *different* trials (subject SBM, 75.4% vs. 64.8% correct; DDL, 78.4% vs. 65.4%; MTS, 77.9% vs. 68.9%; $p < 0.01$ for each subject; $n = 1296$ trials/subject).

3.5. Color experiment without distractors

Subjects performed the dual-task in the absence of distracting stimuli. As plotted in Fig. 2b, the difference in performance between *same* vs. *different* trials was reduced or eliminated for all subjects (SBM, 78.9% vs. 75.6% correct, $p < 0.05$; DDL, 83.3% vs. 78.6%, $p < 0.01$, MTS, 82.1% vs. 81.6%, $p > 0.05$; $n = 1296$ trials/subject).

3.6. Effects of learning

Before data collection, subjects trained on all trial types until stable performance was achieved. We confirmed that the amount of training was adequate by separately analyzing the data from the first and second halves of data collection in all experiments. In the direction of motion and color experiments with distractors, all subjects performed better on *same* trials than on *different* trials in both the first and second halves of the data ($p < 0.05$ for each subject in each half of each experiment). In the direction of motion experiment without distractors, all subjects showed no significant performance difference between *same* and *different* trials in both halves of the data ($p > 0.05$ for each subject in each half). In the color experiment without distractors, MTS showed no performance difference in either half ($p > 0.05$), SBM showed a performance difference that was not significant in the first half but was significant during the second half ($p < 0.05$), and DDL showed a performance difference in both halves ($p < 0.01$). This analysis suggests that additional training would not have changed the outcome of the comparisons in any of the experiments.

4. Discussion

4.1. Summary

We found that observers were better able to concurrently discriminate spatially separate stimuli when those stimuli had common features compared to opposing features. This effect was demonstrated for the two features tested, direction of motion and color. We used overlapping stimuli that were identical in all conditions so that differences in task performance could not be confounded with changes in the stimulus itself or with changes in the spatial distribution of attention. The attentional effect was reduced when the need to filter out overlapping distractors was eliminated.

These results are consistent with our previously reported fMRI findings in which attention to a particular feature of one stimulus was found to increase cortical responses to a spatially separate ignored stimulus sharing the attended feature (Sàenz et al., 2002). This feature-specific response enhancement was observed in multiple early cortical visual areas and suggests that attention improves the processing of stimuli sharing the attended feature throughout the visual field.

If feature-based attention improves the processing of stimuli globally with the attended feature, we reasoned that this should facilitate the distribution of attention across multiple stimuli with common features compared to opposing features. Consistent with that interpretation, subjects in the present experiment reported subjectively that attending to a particular direction of motion or color on one side of the display seemed to make that feature more salient on the other side. Correspondingly, performance was facilitated when observers divided attention across matching features and performance was impaired when observers divided attention across opposing features. Together, the results from our fMRI and psychophysical studies provide complementary physiological and behavioral evidence that feature-based attention does indeed improve the processing of stimuli throughout the visual field that share the attended feature.

Interestingly, the difference in task performance depended on the need to filter out competing stimuli. In the direction of motion experiment, the performance difference was eliminated for all subjects in trials without distractors. In the color experiment, the difference was reduced or eliminated for all subjects in trials without distractors. The different results obtained with and without distractors is not related to overall task difficulty because task performance was in the same range across both sets of trials. Rather, this result is consistent with neurophysiological studies reporting greater effects of attention on individual neurons when multiple stimuli compete for attentional selection within the receptive field (Luck et al., 1997; Moran & Desimone, 1985; Motter, 1993; Treue & Martinez Trujillo, 1999; Treue & Maunsell, 1999). These studies suggest that the role of attention in target selection is greatest in the presence of nearby distractors.

The weakening of the attentional effect in the absence of distractors rules out a potential confounding factor. It would be a trivial finding if subjects performed better when judging matching features simply because they benefited from comparing those features across sides. This was not the case. If such a benefit existed, it would have also been evident on trials without distractors. In the color experiment without distractors, the performance difference was greatly reduced but not eliminated for two out of three subjects. This remaining difference may be interpreted as an estimate of the size of the effect that could be attributed to other factors such as comparing luminances across sides. However, it may also be the case that in the color experiment, feature-specific attention facilitated the discrimination of stimuli with common features even in the absence of distractors.

In all experiments, subjects were instructed to divide attention equally to the left and right sides of the display and perform the two tasks concurrently. However, it is difficult to rule out the possibility that subjects shifted spatial attention back and forth between the two sides and performed the tasks sequentially. The increased performance difference obtained with shorter presentation times (200 ms compared to 500 ms) is consistent with the hypothesis that observers were better able to divide their attention *concurrently* across stimuli with common features compared to opposing features. The shorter presentation time should have been more effective in preventing the observer from switching attention between the two stimuli to avoid this limitation.

4.2. Possible neuronal mechanisms

Our psychophysical results are consistent with a neuronal mechanism by which attention enhances the activity of cortical neurons that encode behaviorally relevant stimulus properties. A *biased competition model* predicts this type of feature-specific attentional modulation (Desimone & Duncan, 1995; Reynolds et al., 1999). The model proposes that multiple stimuli activate competing populations of neurons and attention biases the competition in favor of neurons that encode the features of the attended stimulus. Multiple studies have shown that when a pair of stimuli with different features is presented within a visual cortical neuron's receptive field, the response of the neuron is determined by which of the two stimuli is attended. Attending to the preferred stimulus of the pair increases the neuron's firing rate and attending to the non-preferred stimulus decreases the firing rate. Thus, the effect of attention on a neuron's response (enhancement or suppression) depends on how the features of the attended stimulus match the stimulus selectivity of the neuron. This result has been confirmed for a range of stimuli and visual areas including color stimuli in V2, V4, and IT (Luck et al., 1997; Moran & Desimone, 1985; Reynolds et al., 1999), motion stimuli in MT/V5 (Treue & Maunsell, 1996, 1999) and complex objects in V4 and IT (Chelazzi et al., 1993, 1998, 2001).

Based on these findings, we can speculate about the neuronal mechanisms that mediated our behavioral results. In our divided attention experiments with distractors, overlapping fields of dots with opposing features were presented, presumably activating neurons tuned to both of those features (i.e. upward and downward direction selective neurons or red and green color selective neurons). Attending to one of the fields would have increased the responses of neurons encoding the features of the attended field and suppressed the responses of neurons encoding the features of the overlapping distracting field. Attending to the same feature on both sides of the display may have mutually enhanced the responses of neurons throughout the visual field tuned to the attended feature and suppressed neurons tuned to the opposing feature. This mutual enhancement and suppression may have aided the selection of target fields on our 'same' feature trials, facilitating task performance. Attending to opposing features may have initiated competing effects of enhancement and suppression in both populations of neurons. This interference may have made target selection more difficult on 'different' feature trials, hindering task performance. Thus, a combination of neuronal facilitation and suppression due to attention may have contributed to our psychophysical results.

When the need to filter out (or suppress) overlapping stimuli was removed, the competition between opposing neuronal populations would have been reduced. A subset of the studies listed above also measured the effects of attention when only a single stimulus was presented inside the receptive field (Luck et al., 1997; Moran & Desimone, 1985; Treue & Maunsell, 1999). Another study also compared the effects of attention on responses (V1, V2, and V4) to a target stimulus in the presence or absence of nearby distractors (Motter, 1993). In all cases attentional modulation was reduced in the absence of competing distractors and, in some cases, was eliminated (Luck et al., 1997; Moran & Desimone, 1985). Consistent with these results, in our experiments the performance difference was reduced in the absence of distractors.

Our interpretation requires that the top-down biasing effects of attention be far-reaching enough to affect the processing of a visual object located in the opposite visual hemifield. In support of this, Chelazzi and colleagues showed that searching for a visual stimulus increased the firing rate of IT neurons tuned to that stimulus during a time period *prior* to stimulus presentation (Chelazzi et al., 1993, 1998). This modulation of baseline firing rates was feature-driven and far-reaching because the exact location of the upcoming target was unknown (but the location was limited to a single visual hemifield). Other studies have shown that the modulatory effects of feature-based attention do indeed extend into the opposite visual hemifield (McAdams & Maunsell, 2000; Treue & Martinez Trujillo, 1999).

In particular, Treue and Martinez Trujillo reported feature-specific attentional modulation of stimulus-evoked responses in macaque area MT/V5. In their experiment an ignored random dots stimulus, moving coherently in the preferred direction, was presented inside the receptive field of a directionally tuned neuron. Attention was directed to a second stimulus, outside the receptive field, that either moved in the same or in the opposite direction. On average, neuronal responses to the ignored stimulus increased when the monkey attended the preferred direction and decreased when the monkey attended the opposing direction (compared to passive viewing trials). To account for these results, the authors proposed a *feature-similarity gain model* in which feature-based attention modulates the gain of cortical neurons that are selective for the behaviorally relevant stimulus property. The model emphasizes that the direction of the gain change (decrease or increase) depends on how the attended properties (location or features) match the stimulus selectivity of the neuron and also emphasizes that the modulation will reach neurons with receptive field locations well outside the attended location. Our previous fMRI results as well as the present psychophysical results are consistent with a spatially non-specific mechanism of feature-specific neuronal modulation.

Another explanation for the effectiveness of the distractors, besides competition within receptive fields, may also have to do with task strategy. In the experiments with distractors, observers were required to select one of two overlapping fields of dots with a particular feature and perform a discrimination task on the selected field. In the motion experiment, observers selected a field with a particular direction of motion in order to perform a speed discrimination task and in the color experiment observers selected a field of a particular color in order to perform a luminance discrimination task. Hence, it was primarily the selection of the target field in the presence of the distracting field, rather than the task itself, that required feature-based attention to either direction of motion or color. When the need to filter out the overlapping stimulus was removed, target selection may have been less dependent on feature-based attention. This may have contributed to the reduction of the attentional effect in both experiments without distractors. The amount of feature-based attention that remained after the removal of the distractors may have been different for the two tasks (speed discrimination and luminance discrimination) which could have contributed to the different degrees of effect reduction found in the motion and color experiments without distractors.

4.3. Related human psychophysical studies

The results of our divided attention study indicate that attention to a stimulus feature facilitates the concurrent processing of other stimuli sharing that same feature. This interpretation is consistent with previous psychophysical studies suggesting that observers have a limited ability to attend to more than one spatial frequency at a time (Shulman & Wilson, 1987; Sperling & Melchner, 1978). Our results are also consistent with a study of feature-specific attention (Rossi & Paradiso, 1995) in which observers performed a primary task of discriminating a feature of a foveal grating (spatial frequency or orientation) and a secondary task of detecting a near-threshold grating in the periphery. Although the tasks were not performed concurrently, observers were better at detecting the peripheral grating when its spatial frequency or orientation matched the attended feature in the primary task.

Lee, Koch, and Braun (1999) asked a related question of whether the ability to perform simultaneous tasks depends on the similarity of the two tasks involved. Observers performed a dual-task that involved discriminating dissimilar stimulus dimensions (e.g. form vs. motion) compared to similar stimulus dimensions (e.g. motion vs. motion). They concluded that while it was more difficult to perform two tasks compared to one, it did not matter whether those two tasks were similar or dissimilar. Another recent study (Morrone et al., 2002) reported that performing concurrent tasks on the same stimulus dimension was more difficult than on different stimulus dimensions for tasks involving color vs. luminance contrast discrimination. Our findings are not inconsistent with these results. In our dual-task experiment, subjects always discriminated the same stimulus dimension at a time (either direction of motion or color). What varied was whether the simultaneous tasks involved the same vs. opposing features within a particular stimulus dimension. The competitive neuronal mechanisms described above could apply most specifically to neurons encoding opposing features of a particular stimulus dimension.

4.4. Feature vs. object-based attention

Because two fields of dots moving in the same direction could be perceived as part of a common object viewed through two apertures, our findings could be attributed to an object-based rather than feature-based allocation of attention. Several studies have shown that human observers performed better when concurrently discriminating two features of the same object compared to two features of different objects (Baylis & Driver, 1992; Blaser, Pylyshyn, & Holcombe, 2000; Duncan, 1984; He & Nakayama, 1995). However, whether there exists a clear distinction between object and feature-based attention in the visual system is a difficult question. For many visual objects, it is the sharing of common features that contributes to its ‘objectness’. In our experiment, it is the features (direction of motion or color) that defined the stimuli and we have no evidence that subjects perceived left and right stimuli as part of a common object. Furthermore, in the divided attention experiment left and right stimuli moved at two very different baseline speeds (10 vs. 20 deg/s) or had different baseline luminances, further precluding the binding of the two stimuli as parts of a common object.

4.5. Conclusions

Using a dual-task psychophysical paradigm, we found that subjects were better at detecting changes in a pair of spatially separated stimuli when they share a common feature, such as a direction of motion or color, than when they did not share a common feature. Our results are consistent with a proposed mechanism, called the *feature-similarity gain model*, in which feature-based attention modulates the gain of cortical neurons tuned to the attended feature throughout the visual field (Treue & Martinez Trujillo, 1999). This global feature-based mechanism of attention could play an important role in the process of selecting the location of relevant stimuli for further processing. An increase in the saliency of stimuli with behaviorally relevant features would be useful in identifying relevant peripheral stimuli during visual search for guiding eye-movements, or in grouping stimuli with common features as part of the same object.

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