



Combining spatial and feature-based attention within the receptive field of MT neurons

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ABSTRACT

This study investigates the effects of feature-based attention on responses of direction-selective neurons in the middle temporal area (MT) of macaque visual cortex to attended stimuli inside the receptive field. Redirecting attention between the preferred and null direction of transparent random dot motion patterns caused a mean modulation of responses of ~32%, about half of what was observed when the two directions of motion in the receptive field were spatially separated allowing feature-based and spatial attention to work in concert. This is consistent with models of visual attention that interpret the attentional modulation of a neuron as the combination of all attentional influences, treating stimulus location simply as another feature.

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1. Introduction

Visual attention is a process for enhancing the representation of attended aspects of the sensory input at the expense of unattended information. This endows us with faster and more accurate vision that is of higher spatial resolution and enhanced sensitivity for fine changes. Perceptually attentional modulation seems to manipulate the very appearance of our environment, increasing the apparent contrast of attended stimuli (Carrasco, Ling, & Read, 2004; Treue, 2004) and enhancing their perceptual strength along a multitude of dimensions (e.g. Anton-Erxleben, Henrich, & Treue, 2007; Lankheet & Verstraten, 1995; Liu, Fuller, & Carrasco, 2006; Turatto, Ves-covi, & Valsecchi, 2007).

The physiological correlate of these effects appears to be an enhanced gain of neurons in visual cortex tuned to the stimulus dimensions that are relevant in the momentary context and preferring features (such as a particular stimulus location, direction, and orientation) that are currently attended. Correspondingly the sign and magnitude of attentional modulation of individual neurons are well predicted by the similarity between the attended stimulus properties and the preference of a given neuron for these features. While most studies of the neurophysiological correlate of attentional modulation have focused on spatial attention this feature-similarity gain

model was developed as a consequence of observing a direction-specific gain enhancement of neurons in area MT of macaque visual cortex across the visual field when the animal was attending to a stimulus moving coherently in one direction (Martinez-Trujillo & Treue, 2004; Treue & Martinez-Trujillo, 1999). Such a feature-based response modulation of neurons, even though spatial attention was directed far outside their receptive field, was subsequently also observed in recordings in area V4 (Bichot, Rossi, & Desimone, 2005; McAdams & Maunsell, 2000), as well as fMRI and EEG studies (Saenz, Buracas, & Boynton, 2002; Stoppel et al., 2007) and psychophysical experiments (Saenz et al., 2002) and is consistent with the results of other recording studies of the effects of feature-based attention in the ventral processing pathway of primate visual cortex (Chelazzi, Duncan, Miller, & Desimone, 1998; Chelazzi, Miller, & Desimone, 1993; Haenny, Maunsell, & Schiller, 1988; Haenny & Schiller, 1988; Mirabella et al., 2007; Motter, 1994a, 1994b).

While single-cell recording studies of spatial attention have addressed the changes in receptive field profiles (Anton-Erxleben, Stephan, & Treue, in press; Connor, Gallant, Preddie, & Van Essen, 1996; Connor, Preddie, Gallant, & Van Essen, 1997; Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006; Womelsdorf, Anton-Erxleben, & Treue, 2008) when attention is directed in or near the receptive field, studies of feature-based attention have often maintained attention far outside the receptive field. The notable exception is a recent study by Wannig, Rodriguez, and Freiwald (2007), who have cued macaque monkeys to direct their attention onto one of two superimposed, transparently counter-rotating random dot surfaces. They interpret their finding of a non-spatial attentional modulation depending on the local direction of motion of the attended

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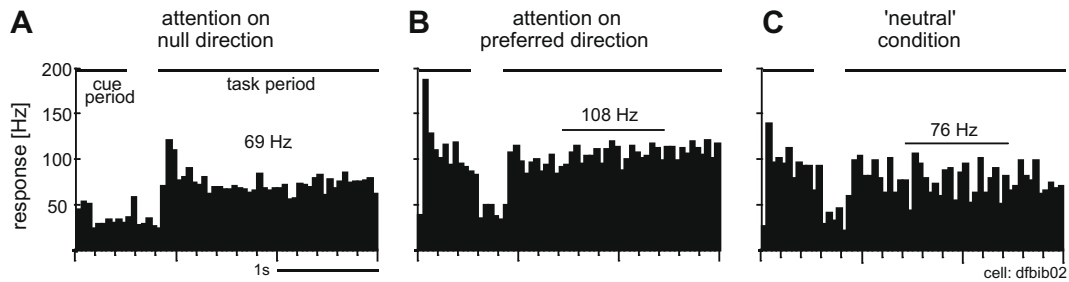


Fig. 1. Responses of a single cell in the three behavioral conditions of task 1. The x-axis represents time and the y-axis average firing rate across trials in 50 ms bins. The panels show post stimulus time histograms of the cell during the cue presentation, the task phase (when the transparent stimulus was presented) and the blank period in between. In each task period transparent motion (preferred and null direction) was presented inside the receptive field. In condition A attention was directed towards the null direction and in condition B towards the preferred direction. In condition C attention was on a dot at the fixation cross. The firing rate shown in each panel represents the average response rates during the interval indicated by the horizontal line (including only hit trials where the behaviorally relevant target change occurred after the analyzed interval). The stimulus during the cue period moved in the null direction in condition A and in the preferred direction in the other two conditions.

dot pattern as surface-based attention, while at least some of the data could also be accounted for by an expanded feature-similarity gain model of attention (Treue & Katzner, 2007).

Here we report the effects of feature-based attention directed into the receptive field of MT neurons in tasks designed to either isolate the effects of attention to a particular motion direction or to combine it with spatial attention. We find strong attentional effects based on the attended direction which was further enhanced by combining it with the modulation caused by selectively attending to one of two spatially separated patterns within the receptive field.

2. Methods

Stimuli: Task 1 was designed to study attentional modulation based solely on the direction of motion in the absence of any changes in spatial attention. The transparent motion stimulus consisted of two spatially superimposed random dot patterns (dot size 0.03° , density: 3 dots/deg²) moving in the preferred and null direction for the cell under study. The two dot patterns were red or green, respectively (approximately isoluminant) to make the perceptual separation easier (Croner & Albright, 1999) but the two possible color-direction combinations were randomized. Transparent motion stimuli pose a particular challenge for the visual system as they require the extraction and encoding of more than one stimulus property at a given visual field location and in that signal-to-noise ratios cannot be improved by enlarging the area of spatial averaging. Responses in area MT to the combination of multiple directions of motion in the receptive field fall in between the responses to the individual directions in isolation (Snowden, Treue, Erickson, & Andersen, 1991; Treue, Hol, & Rauber, 2000).

Task 2 was designed to investigate the effect of combining spatial location and motion direction. The two moving patterns were spatially separated half circles of moving white dots, and were placed side-by-side to form a circle, separated by a gap (1/10 of the stimulus diameter, see Fig. 3a). In both tasks the size (3–10° diameter), direction, and speed (2–20°/s) of the patterns were adjusted to the preferences of each recorded cell. In Task 2 the two half circles were aligned parallel to the preferred direction of the cell. The same dot density was used for the surfaces in tasks 1 and 2. Because of the smaller stimulus area in Task 2 that meant that fewer dots were present in the receptive field. This is unlikely to have any effect on responses given that MT neurons show response saturation at low number of dots in the receptive field (Snowden et al., 1991, 1992).

Behavioral task: tasks 1 and 2 were carried out in separate blocks, but within a given block all trial conditions were interleaved. In task 1 the monkey was instructed by a moving pattern which direction was relevant (target) in a given trial, and in task 2 the location of a static pattern indicated the relevant location (target). The other pattern was irrelevant (distractor). At the beginning

of each trial the respective cue was presented for 500 ms and was separated from the onset of the target and distractor stimuli by a gap of 350 msec¹. During the following task period both target and distractor could change speed (duration: 200 ms, 340–2660 ms after onset, 70–120% faster than the base speed), and the monkey was rewarded only when he responded to a speed change of the target by releasing a lever. In a 'neutral' condition the monkey had to respond to a color change at the fixation cross. Failure to respond within the reaction time window (200–600 ms after the end of the speed change), responding to a change in the distractor or deviating the gaze by more than 1° from the fixation cross aborted the trial without reward. The monkey's performance was 86% (task 1), and 73% (task 2) of those trials that were not aborted due to eye movements.

Data analysis: Our recording methods have been described elsewhere (Treue & Maunsell, 1999). Cells were determined to be in MT by their directionality, receptive field position and size, and by the position of the electrode in the brain. Response rates were determined by averaging the firing rates across trials for 1 s starting 600 ms after task period onset to exclude motion onset responses (see Fig. 1). Only correctly completed trials and within those only trials where no stimulus change occurred within the period used for determining the response rate were included in the analysis. Data analysis was restricted to 46 cells for which more than 8 trials per condition were recorded. To quantify attentional modulation between two different attentional conditions an attentional index $(R_p - R_N)/(R_p + R_N)$ was calculated (R_p = response when attending to preferred direction, R_N = response when attending to null-direction). *t*-Tests were used throughout to test for significant shifts of the index distribution from zero (no attentional modulation).

3. Results

3.1. Attention to motion direction

In task 1 the monkey had to attend either to the preferred direction, the null direction, or to a dot at the fixation cross. Fig. 1 depicts the responses of a typical MT cell under these three attentional conditions.

When attention was directed to the null direction (Fig. 1A) the firing rate was lowest (mean: 69 Hz). Under the same stimulus conditions but with attention directed to the cell's preferred direction (Fig. 1B) the firing rate increased substantially (108 Hz, an

¹ This delay is long enough for a decay of the activity evoked by the cue. Therefore a potential influence on the following stimulus period would consist of an adaptation effect that would reduce responses in the attention on preferred direction and vice versa for the attention on null direction. Rather than accounting for our observation such an effect would reduce the attentional modulation observed.

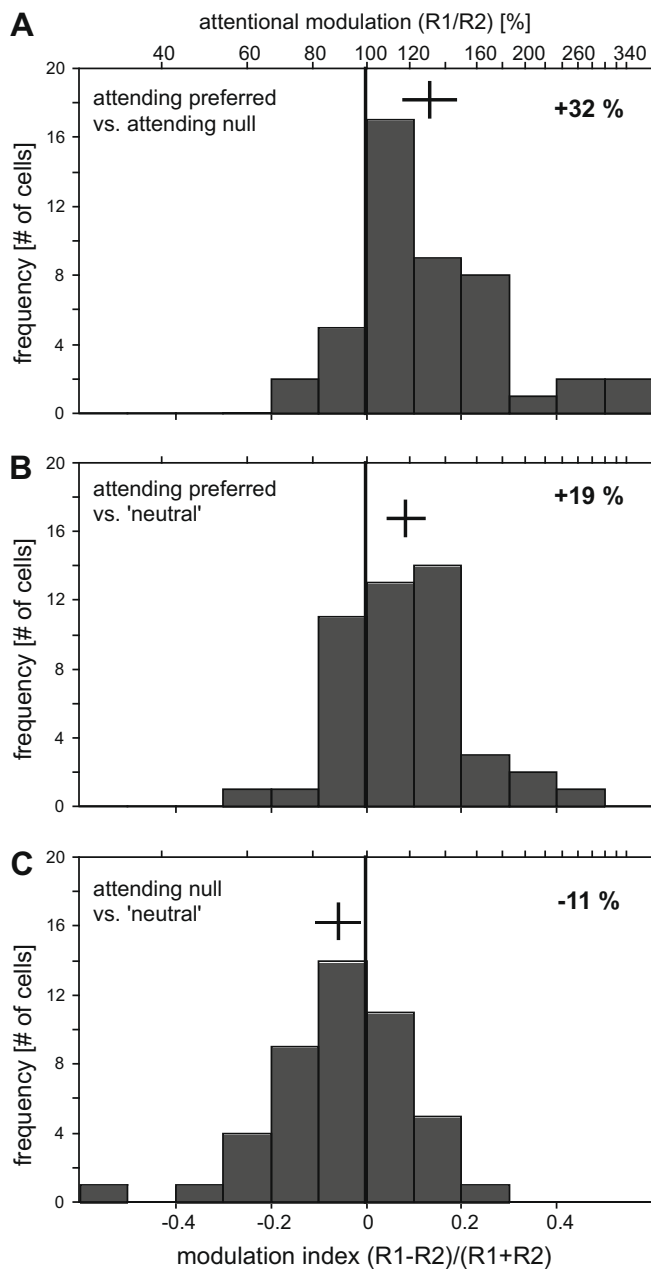


Fig. 2. Attentional modulation using transparent patterns. Distribution of the attentional modulation for the population of 46 MT cells included in the analysis. The top x -axes represents the attentional modulation as a ratio (R_P/R_N), the bottom x -axes as the attentional index ($(R_P - R_N)/(R_P + R_N)$). The central vertical line represents a ratio of 100% and an index of 0, i.e. no difference between the responses in the two conditions while positive index values represent cells for which R_P was larger than R_N . The cross above each histogram represents the geometric mean of the ratio and the mean index value and the associated 95% confidence interval. (A) Comparing the firing rates when attention is on the preferred versus the null motion direction (Fig. 1A vs. B) results in a mean index of 0.14 ± 0.05 , corresponding to a response enhancement of 32% when attending to the preferred direction. Note that some cells doubled or tripled their firing rates when switching attention from the null to the preferred direction. (B) Comparing the firing rates when attention is on the preferred direction inside the receptive field versus when it is outside the receptive field (Fig. 1A vs. C), the mean index is 0.09 ± 0.04 , corresponding to a 19% higher response when attention was directed towards the preferred direction inside the receptive field. (C) When redirecting attention from outside the receptive field to the null motion direction inside the receptive field, the distribution is shifted significantly to negative values (mean: -0.06 ± 0.05), corresponding to an 11% inhibition of the response when attention was directed towards the null direction inside the receptive field.

increase of 57%). Directing attention to the fixation point (Fig. 1C) resulted in an intermediate firing rate (76 Hz). This means that

shifting attention from outside the receptive field to the preferred direction inside the receptive field increased responses by 42%, while shifting attention from outside to the null direction inside the receptive field responses decreased them by 9%. This pattern of results was typical for the attentional modulation seen across our sample of cells (Fig. 2).

Comparing conditions when attention was directed to the preferred versus the null direction (Fig. 2A) results in a distribution of attentional modulation that is shifted significantly ($p < 0.0001$) to positive values. That is, on average responses to transparent motion were 32% higher when attention was directed to the preferred direction versus when attention was directed to the null direction. Comparing the responses in the 'neutral' condition (when attention was directed onto the fixation point) with the condition when attention was on the preferred direction the distribution is shifted to positive values ($p < 0.0001$), corresponding to a response enhancement of 19% (Fig. 2B). When attention was shifted from the 'neutral' condition to the null direction inside the receptive field the distribution is shifted to negative values ($p < 0.026$), i.e. the cells' responses were reduced by 11% (Fig. 2C). Therefore, the attended motion direction in an MT receptive field can be the basis of attentional response modulation, enhancing or suppressing responses compared to a 'neutral' condition. It should be noted though, that the attentional state of the animal in the fixation condition is much less stringently defined than in the condition of eccentric attention to a stimulus. The apparent balance of inhibition and excitation is thus dramatically influenced even by rather small changes the firing rate in the fixation condition. A much more reliable measure of attentional modulation is provided by the comparison underlying Fig. 2A since the two attentional conditions are very comparable in every behavioral aspect.

3.2. Attention to location

To relate the observed feature-based attentional modulation to spatial attention two oppositely moving, and spatially separated patterns were presented inside the cell's receptive field (Fig. 3A).

Comparing the responses of 45 cells when the target was the stimulus moving in the preferred to when it was the stimulus moving in the null direction, revealed a strong attentional modulation (mean response enhancement 69% (Fig. 3B; $p < 0.0001$). This attentional modulation is composed of an enhancement (mean 43%, 'neutral' condition compared with preferred motion target), and an inhibition (mean 16%, 'neutral' condition compared with null motion target). For 31 cells data were collected in tasks 1 and 2, allowing a direct comparison. We found a positive correlation between the strengths of attentional modulation (correlation coefficient: 0.44, Fig. 3C), i.e. cells which are modulated strongly when attention is based on spatial location and direction (task 2) are also modulated strongly when attention is based on motion direction alone (task 1).

4. Discussion

In summary, our results show that redirecting attention between two spatially coincident motion directions inside the receptive field modulates direction-selective responses in cortical area MT on average by 32%. When switching attention between the preferred and null motion direction presented at different spatial locations the response modulation is about twice as strong (69%) suggesting the combination of equally strong featural and spatial attentional effects. Our data also show that the strength of spatial and feature-based effects in a given cell are correlated, suggesting that the two modulations are not independent but might rather

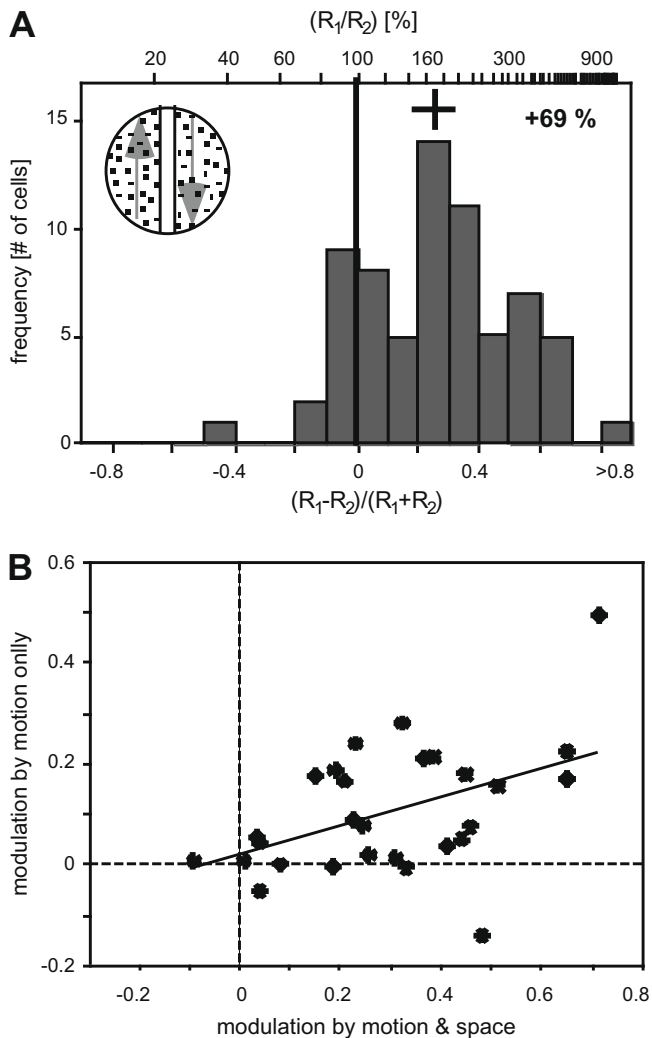


Fig. 3. Combining location-based and direction-based attentional modulation (using spatially separated, non-transparent stimuli): Histogram of attentional modulation for a population of 45 MT cells comparing the firing rates recorded when the target pattern moved in the preferred direction of the cell versus when it moved in the null direction. The distribution is significantly shifted to positive values with a mean index of 0.26 ± 0.06 , corresponding to a 69% stronger response when attention was directed towards the pattern moving in the preferred direction. Correlation of the modulation index in tasks 1 and 2, for those 31 MT cells for which both data sets were recorded. The straight line is the least square fit through the data (slope: 0.24; correlation coefficient: 0.44).

reflect a unified attentional system in which the attended location is just another feature for which the cell is tuned to.

4.1. Influence of the perceptual surface depth order?

Not only does area MT contain a high proportion of directional selective neurons but two-thirds of the cells are also selective for binocular disparity, or depth (Maunsell & Van Essen, 1983). As transparent patterns, even in the absence of depth cues normally perceptually segregate into a ‘front’ and ‘back’ surface one might imagine that this perceptual segregation has a neuronal correlation in MT in that neurons preferring near disparities might respond to the ‘front’ surface’s direction and neurons preferring far disparities responding to the ‘back’ surface’s direction (Krug, 2004; Krug, Cumming, & Parker, 2004). One might further suppose that attention enhances responses having a preferred depth aligned with the perceived depth position of the attended surface and reducing re-

sponses of those neurons for which this is not the case. Such an effect would not generate the shifted attentional index distribution we have observed as attending to a particular direction or surface would enhance and suppress one half of the neurons, respectively. Instead we see an enhancement whenever the attended direction is the preferred direction and a suppression for the opposite direction.

4.2. Non-spatial, feature-based attention

When shifting attention between stimuli spatially separated inside the receptive field the neural response is dominated by the relevant stimulus (Luck, Chelazzi, Hillyard, & Desimone, 1997; Moran & Desimone, 1985; Motter, 1994a, 1994b; Treue & Maunsell, 1996; Treue & Maunsell, 1999). It has been suggested that this reflects a receptive field shrinking around the target, excluding irrelevant stimuli (Moran & Desimone, 1985). While an attentional influence on the spatial tuning, i.e. the receptive field profile of V4 and MT neurons has been documented (Anton-Erxleben et al., in press; Connor et al., 1996; Connor et al., 1997; Womelsdorf et al., 2006, 2008) such a spatial mechanism could not account for the response modulation with the transparent patterns in our task 1 though, as shrinking of the receptive field would not selectively exclude the distractor. Rather, one has to assume a mechanism that can act solely on the basis of motion directions.

Such a feature-based mechanism can help to solve the difficult task of the visual system to segregate different motion directions at the same spatial location. Many studies of sensory processing have collected evidence for processes that combine signals within the RF (Qian & Andersen, 1994; Recanzone, Wurtz, & Schwarz, 1997; Snowden et al., 1991; Treue et al., 2000). Attention on the other hand seems to be a mechanism well suited for aiding in the segregation by enabling the visual system to enhance the representation of one direction while suppressing the influence of other directions.

Correspondingly the ability of feature-based attention to differentially influence stimuli even when they fall within the same spatial aperture has been found in many imaging studies in humans using positron emission tomography (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990), magnetic resonance imaging (Liu, Larsson, & Carrasco, 2007a; O’Craven et al., 1997; Saenz et al., 2002), event-related potentials (Hopf, Boelmans, Schoenfeld, Luck, & Heinze, 2004; Müller et al., 2006; Pinilla, Cobo, Torres, & Valdes-Sosa, 2001; Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998), and psychophysics (Katzner, Busse, & Treue, 2006; Lankheet & Verstraten, 1995; Liu, Stevens, & Carrasco, 2007b; Reynolds, Alborzian, & Stoner, 2003).

In the context of the feature-similarity model the feature-based attentional modulation we observed might reflect the direct effect of an enhancement of cells preferring the attended direction and a suppression of those cells for which the attended direction corresponds to the anti-preferred direction. Alternatively the modulation we observed in MT might be the result of a feature-selective modulation of the two populations V1 neurons providing input to the given MT neuron, one tuned for the preferred and the other for the anti-preferred direction of the MT neuron (providing excitatory and inhibitory inputs, respectively). Because V1 neurons have been found to be rather uninfluenced by the presence of their anti-preferred direction (Snowden et al., 1991) the two populations provide distinct neural representations of the two surfaces in transparent motion that can be separately targeted by feature-based attention.

4.3. Spatial and non-spatial effects

Similar to many studies in visual cortex we found a strong attentional effect when target and distractor were both inside

the RF but spatially separated. This attentional modulation is about twice as strong as the one we observed when the target and distractor shared the same spatial location. While the somewhat higher error rate in our task 1 suggest that the transparent condition was less difficult for the animal this is likely to provide at best a small contribution to the difference in attentional modulation since both tasks were very demanding and required a very high level of attention. Instead, the finding of Treue and Martinez-Trujillo (1999) that spatial and non-spatial effects are about equally strong and additive when attention is switched between inside and outside of the receptive field of MT neurons suggests that the doubling of the attentional modulation observed in the current study similarly reflect the combination of a feature-based modulation (observed in isolation in the transparent case) with an effect of spatial attention (that can only differentially affect the target and distractor in the non-transparent case). In the framework of the feature-similarity gain model the larger attentional modulation for spatially separated stimuli is interpreted as an effect of spatial attention on the inputs to MT. Within area MT such an effect would not be predicted by the feature-similarity gain model, since there is no systematic difference in the sensitivity of the two locations. But the input to MT cells comes from a mosaic of input neurons in V1 with much smaller RFs. Some of these neurons have RFs overlapping one stimulus and other neurons have RFs overlapping the other stimulus. Because of the effects of spatial attention in V1 the responses of those neurons encoding the attended stimulus will be enhanced and thus provide a stronger input than those encoding the unattended stimulus. This will create an attentional modulation of the inputs that will combine with the feature-based modulation based on the attended direction. The basis of the spatial attention effect is likely to be the shift of the receptive field profile observed in previous studies in MT (Anton-Erxleben et al., in press; Womelsdorf et al., 2006, 2008) under very similar conditions.

Note that the attentional enhancement and suppression (when attending to the preferred vs. the null direction, respectively) relative to the fixation condition in the transparent motion condition are of similar sizes (Fig. 2) while the enhancement was much stronger than the suppression when the stimuli in the RF were spatially separated. This observation matches the predictions of the feature-similarity model: Comparing a condition where attention is on the fixation point with the condition where attention was directed at the preferred direction inside the RF yields a large attentional enhancement because both, the enhancement of switching attention to the preferred direction as well as the enhancement of switching attention to the preferred location (inside the RF, rather than outside) combine. In the case of switching attention into the RF and onto a stimulus moving in the null-direction this combination leads to a partial cancellation because the enhancement of switching attention to the preferred location is partially offset by the suppression of switching feature-based attention to the null direction.

The strength of attentional modulation we observed in the various conditions could therefore be interpreted as reflecting the various levels of feature-similarity according to the feature-similarity model or in the context of the biased competition model (Desimone & Duncan, 1995; Reynolds, Chelazzi, & Desimone, 1999) if the competing neuronal subpopulations that are the core of that model can be groups of direction-selective input neurons that can differ not only in their receptive field positions but also in their preferred directions. Our findings are in agreement with the recent report of Wannig et al. (2007) which have also investigated attentional modulation in area MT using transparent motion stimuli albeit in a more complex paradigm. Their paradigm was adapted from one developed by Valdes-Sosa, Cobo, and Pinilla (2000) to investigate surface-based attentional modulation while our study

focuses on the similarity of attentional modulation by spatial and featural processes. Our findings are most parsimoniously accounted for by a mechanism of feature-based attention, akin to the feature-similarity gain model (Treue & Martinez-Trujillo, 1999) but the findings of Wannig et al. (2007) suggest that such a mechanism could contribute to a more elaborate attentional system for selectively enhancing the representation of surfaces or objects, rather than individual features (Katzner, Busse, & Treue, 2005; Melcher, Pappathomas, & Vidnyánszky, 2005; Pinilla et al., 2001; Treue & Katzner, 2007; Valdes-Sosa et al., 1998, 2000). A full discussion of how surface and object-based attention requires a more sophisticated attentional system than feature-based attention goes beyond the scope of this brief communication but can be found in the studies cited above.

Together these studies document that the total attentional modulation in the visual system represents the combination of spatial and non-spatial mechanisms which work both within the receptive fields as well as beyond it to create a representation of the visual input that emphasizes those aspects that are of particular behavioral relevance at the given moment (Maunsell & Treue, 2006).

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