Neuron

Volume 72
Number 6
December 22, 2011

www.cellpress.com

Multifocal Attention Filters Targets from Distractors

Reviews:
Sodium Leak Channels
Auditory Developmental Plasticity

Neuron
Article

Multifocal Attention Filters Targets from Distracters within and beyond Primate MT Neurons' Receptive Field Boundaries

Robert Niebergall,[1,2] Paul S. Khayat,[3] Stefan Treue,[2,4] and Julio C. Martinez-Trujillo[1,*]
[1]Cognitive Neurophysiology Laboratory, Department of Physiology, McGill University, Montreal, QC H3G 1Y6, Canada
[2]Cognitive Neuroscience Laboratory, German Primate Center, 37077 Goettingen, Germany
[3]Department of Psychology, University of Montreal, Montreal, QC H3C 3J7, Canada
[4]Bernstein Center for Computational Neuroscience Goettingen, 37073 Goettingen, Germany
*Correspondence: julio.martinez@mcgill.ca
DOI 10.1016/j.neuron.2011.10.013

SUMMARY

Visual attention has been classically described as a spotlight that enhances the processing of a behaviorally relevant object. However, in many situations, humans and animals must simultaneously attend to several relevant objects separated by distracters. To account for this ability, various models of attention have been proposed including splitting of the attentional spotlight into multiple foci, zooming of the spotlight over a region of space, and switching of the spotlight among objects. We investigated this controversial issue by recording neuronal activity in visual area MT of two macaques while they attended to two translating objects that circumvented a third distracter object located inside the neurons' receptive field. We found that when the attended objects passed through or nearby the receptive field, neuronal responses to the distracter were either decreased or remained unaltered. These results demonstrate that attention can split into multiple spotlights corresponding to relevant objects while filtering out interspersed distracters.

INTRODUCTION

Visual attention has been classically described as a spotlight that enhances the processing of objects at the attended location (Posner et al., 1980). In some circumstances, however, an organism must simultaneously attend to several objects located at different positions and separated by irrelevant distracters (e.g., an animal keeping track of predators while ignoring nearby herd members, or a hockey goalie keeping track of several players in the opposite team while ignoring his team mates). It has been proposed that in these situations, the spotlight of attention may split into multiple foci corresponding to the relevant objects and excluding distracters positioned in between (Castiello and Umiltà, 1992), or may zoom out to include the relevant objects but also the interspersed distracters (Eriksen and St James, 1986), or may rapidly switch from one relevant object to another (Posner et al., 1980). The distinction between these different alternatives has been the matter of controversy among studies of attention (see Jans et al., 2010 and Cave et al., 2010).

Previous studies in humans using event-related potentials (ERPs) and functional magnetic resonance imaging (fMRI) have reported that during tasks that require simultaneously attending to several objects brain signals evoked by attended objects are enhanced while signals evoked by distracters positioned in between are suppressed (Drew et al., 2009; McMains and Somers, 2004; Morawetz et al., 2007; Müller et al., 2003a). Other studies, however, have reported that under similar conditions brain signals evoked by attended objects but also by interspersed distracters are enhanced (Barriopedro and Botella, 1998; Heinze et al., 1994; McCormick and Jolicoeur, 1994; Müller et al., 2003b). The results of these two groups of studies support the split of attention into multiple independent foci, and the zooming of a single attentional spotlight, respectively. This controversy may reflect two different working modes of attention depending on the stimuli and task used in each study, or limitations in some of the studies' ability to detect multiple foci of attentional modulation within visual cortical maps.

One way to clarify this controversy and obtain further insight into the mechanisms underlying attention to multiple objects in the primate brain is by examining the responses of single neurons in the visual cortex of monkeys during tasks requiring simultaneously attending to several objects in a visual display while ignoring interspersed distracters. Importantly, this approach has the advantage over ERP and fMRI studies that it allows testing whether and how physiological properties of visual neurons such as receptive field (RF) boundaries, and selectivity for visual features influence subjects' ability to split or zoom out the spotlight of attention in visual cortex.

We recorded the responses of single neurons in the middle temporal visual area (MT) of two rhesus monkeys during three different conditions. In the first, *tracking*, animals covertly attended to two stimuli that translated across a projection screen (translating RDPs) circumventing a third behaviorally irrelevant stimulus positioned inside the neurons' RF (RF pattern). In the second, *attend-RF*, animals attended to the RF pattern while ignoring the translating RDPs. In the third, *attend-fixation*, animals attended to a central "fixation" spot and ignored all

RDPs. We found that during *tracking* neuronal responses were strongly decreased when the translating RDPs passed nearby the RF pattern relative to *attend-RF*. Furthermore, during *tracking* responses were either similar or decreased relative to *attend-fixation*. These results support a split of the attentional spotlight during multiple object tracking.

RESULTS

Behavioral Performance

We recorded the performance of two rhesus monkeys during three different tasks, *tracking*, *attend-RF*, and *attend-fixation* (Figure 1C; Experimental Procedures). During *tracking*, the animals reacted to a speed change in one of the translating RDPs while ignoring similar changes in the RF pattern. During *attend-RF*, they reacted to changes in the RF pattern while ignoring changes in the translating RDPs. During *attend-fixation*, they reacted to changes in the luminance of the fixation spot while ignoring any change in the RDPs. About a third of the trials contained changes in a distractor stimulus preceding the target change. Therefore, if the animals reacted to the first change in any element of the display the overall detection (hit) rate would be 70%. Both animals performed considerably above this level (see below).

To test whether during *tracking* the animals attended to both translating RDPs, we quantified the hit rate as well as the reaction times (RTs) corresponding to changes in each pattern. In each *tracking* trial, speed changes occurred with equal probability (0.5) in each translating RDP, therefore if the animals decided to attend to only one pattern while ignoring the other the hit rate in tracking trials would be ~50%. Figure 2A shows hit rates corresponding to both translating RDPs (upper and lower relative to the vertical meridian). Both animals generally performed above 70% for both RDPs ($p < 0.0001$, Wilcoxon signed rank tests). Moreover, the distributions of performance differences between hit rates corresponding to both RDPs in individual sessions were centered at zero (Figure 2B, monkey Se: $p = 0.7$; monkey Lu: $p = 0.1$, Wilcoxon rank sum test), suggesting that within a session the hit rates corresponding to both patterns were similar.

We examined mean RTs to changes in each RDP across individual sessions (Figures 2C and 2D). They were similar for monkey Se ($p = 0.37$, t test, *mean difference* = −1.8 ms) but slightly different for monkey Lu ($p < 0.0001$, t test, *mean difference* = 3.6 ms). More importantly, we tested whether within individual sessions animals reacted faster to changes in one of the two translating RDPs. Figure 2E shows that p values for comparisons between the RTs corresponding to both RDPs within a session are above 0.05 (unpaired t test); thus, the animals reacted similarly fast to changes in each translating RDP.

To further test whether during *tracking* the animals attended to both translating RDPs we trained Se in a task during which 80% of the speed changes occurred in one pattern (*80-target*) and 20% in the other (*20-target*). We hypothesized that in this task the animal should predominantly attend to the *80-target*, yielding lower hit rates and higher RTs for changes in the *20-target*. Indeed, across 12 sessions the hit rate was 90% for the *80-target* and dropped to 72.4% for the *20-target* (Figure 2F, $p = 0.00018$, Wilcoxon rank sum test). Accordingly, the average RT increased by 24 ms for changes in the *20-target* (398 ms) relative to changes in the *80-target* (374 ms, $p < 0.0001$, unpaired t test).

Interestingly, for Se hit rates and RTs corresponding to changes in the *80-target* were similar to those corresponding to both targets in the main *tracking* task (*50-targets*, Figure 2F, dashed rectangles, *mean* = 374 ms). This suggests that the *80-target* and the *50-targets* of the main task were similarly attended. On the other hand, for the *20-target* it is possible that the animal: (1) devoted some attention to it (i.e., split attentional resources following the target change probability),

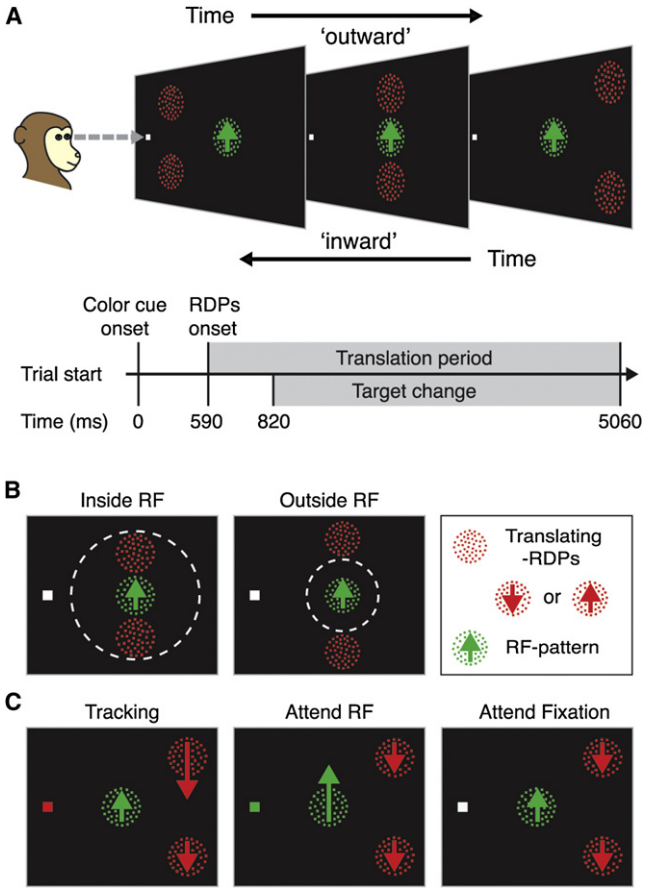

Figure 1. Task Layout

(A) Trial sequence. The animals' gaze (gray arrow) was centered on the fixation spot (white square). During outward trials, the translating RDPs (red) moved eccentrically toward the periphery. During inward trials, they moved concentrically toward the fixation spot. Local dots in the RF pattern (green) always moved in the cells' Pr direction (upward arrow). In the translating RDPs they could move in the Pr or AP direction (downward arrow). The timing sequence of events is shown on the bottom.

(B) Stimulus configurations. In one group of neurons (inside RF) the translating RDPs' trajectories crossed the RF (dashed circle). In the other group (outside RF) they passed nearby the RF.

(C) Experimental conditions. The color of the fixation spot instructed the animals to attend either to the translating RDPs (*tracking*), or to the RF pattern (*attend-RF*) and to detect a change in the local dots' speed (large arrow), or to the fixation spot (*attend-fixation*).

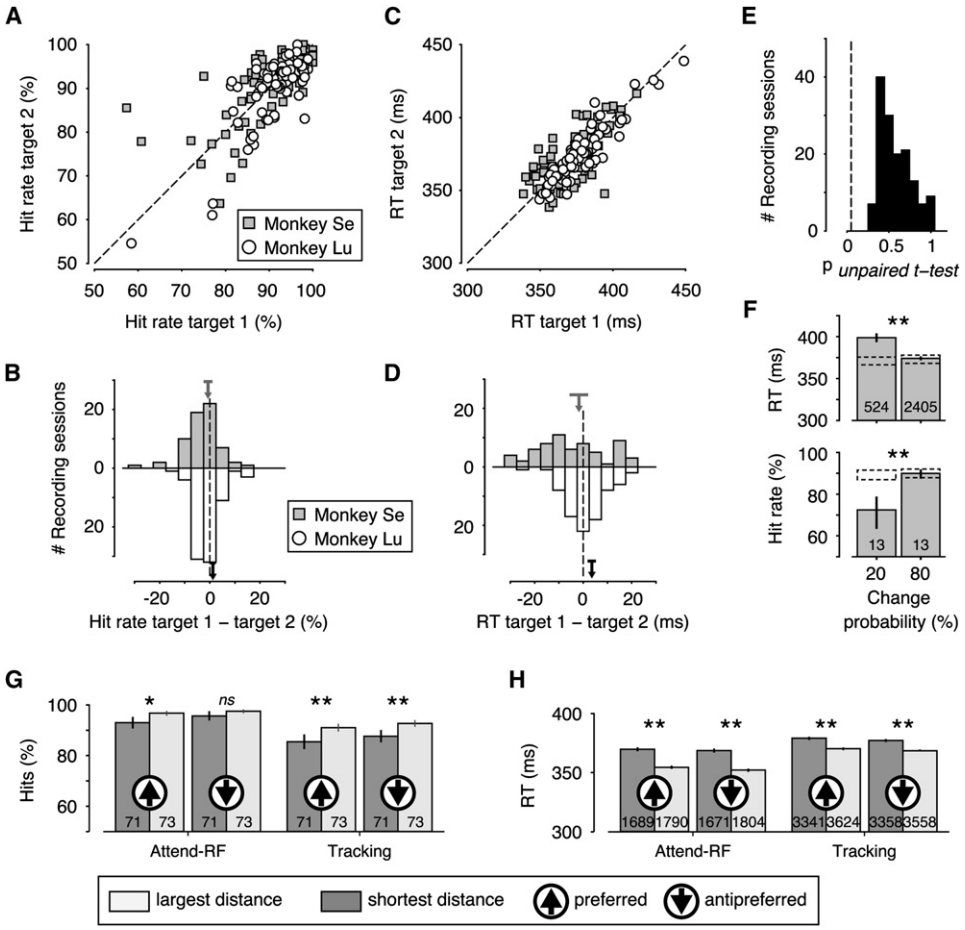

Figure 2. Behavioral Performance

(A) Hit rates for change detections in the two translating RDPs (Lu: n = 84; Se: n = 63). Each point represents data from one recording session.

(B) Distribution of hit rate differences between the two targets for the data shown in (A). The arrows indicate the mean difference.

(C and D) (C) Average reaction times (RTs) for change detections in the two patterns and (D) the distributions of their differences.

(E) Comparison of RTs to changes in both translating RDPs in individual sessions. The histogram displays p values (unpaired t test) across all comparisons. The dashed line represents the significance level (0.05).

(F) Control experiment with monkey Se. The average RTs (top) and hit rate (bottom) follow the probability distributions (0.8 or 0.2) for changes in the two targets. The dashed rectangles show the corresponding means (±95% CI) in the main experiment.

(G and H) (G) Hit rates and (H) RTs as a function of distance between the translating RDPs. All error bars represent 95% CI. Sample sizes are indicated. *ns*, nonsignificant, *p < 0.01, **p < 0.0001, unpaired t test.

or (2) ignored it and exogenously switched attention from the *80-target* toward it when a change occurred. Both strategies could explain the low hit rate and longer RT associated with the *20-target*. Importantly, if one considers strategy "b" as the one the animal adopted the RT differences between *80-* and *20-target* trials could provide an estimate of the time required for the animal to switch the spotlight of attention (~24 ms). This time is shorter than the lowest duration of task-driven attention shifts in humans (35 ms, Horowitz et al., 2009). Along the same line, we reasoned that in the main *tracking* task, if the animal had switched attention back and forth between the two *50-targets* the distribution of RTs would have been a mix of the *80-* and *20-target* RTs' distributions. This is because when a change occurred in the target where the spotlight was momentarily allocated, the RT would resemble that of the *80-target*, and when the change occurred in the momentarily unattended target the RT would resemble that of the *20-target*.

To test this hypothesis, we pooled the RTs of all trials corresponding to the *20-target* across the 12 sessions (n = 524) with a similar number of randomly selected trials of the *80-target* (n = 524 out of 2,405) and obtained a mixed distribution (80/20-mixed). These data were compared against a similar number of trials of the *50-targets* across 12 randomly selected recording sessions in the same animal. The 80/20-mixed distribution mean (378 ms) was significantly larger than the one of the 50-distribution (370 ms, $p < 0.05$, unpaired t test). These results strongly suggest that during *tracking* the animals simultaneously attended to both *50-targets* rather than switching back and forth a single spotlight of attention between them.

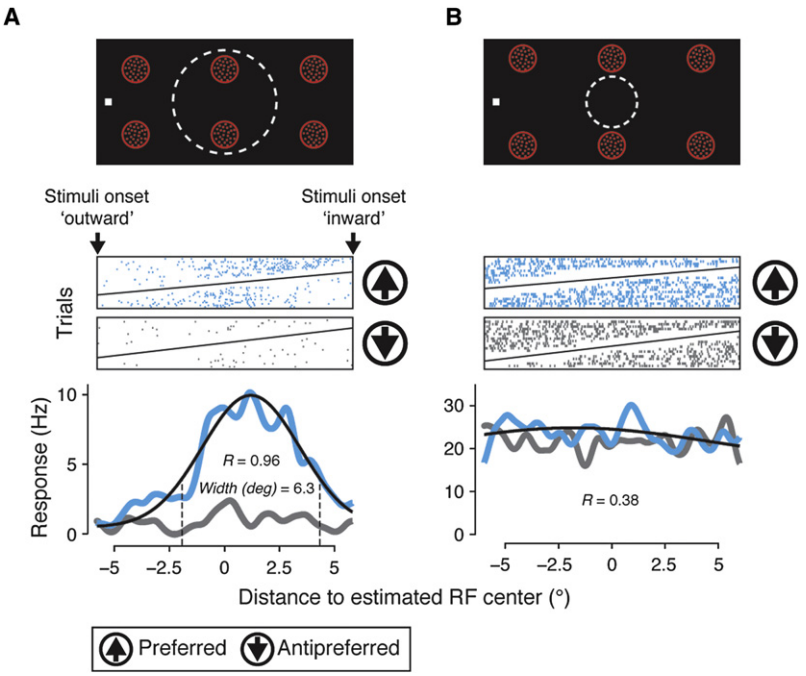

Figure 3. Cell Examples

(A) Single cell example in the inside RF configuration. The top panel illustrates different positions of the translating RDPs (red) relative to the RF (dashed circle). Neuronal responses were obtained while the animals detected a luminance change in the fixation spot and ignored the RDPs. Spike-raster plots (middle) and average responses (bottom) as a function of Pr (blue) and AP (gray) translating RDPs' position. Average responses to the Pr patterns were fit with a Gaussian function (black line).

(B) Cell example in the outside RF configuration. Symbols are the same as in (A).

During the *attend-RF* condition the mean hit rate and RTs (±95% confidence intervals) were 94% ± 1.6% and 370 ± 6 ms for Lu, and 98% ± 0.9% and 358 ± 6 ms for Se, indicating that in this condition they devoted attention to the RF pattern and ignored the translating RDPs. During *attend-fixation* the mean hit rates and RTs were 99.6% ± 0.14% and 308 ± 3 ms for Lu, and 99% ± 0.03% and 322 ± 4 ms for Se. The lower hit rate and longer RTs across sessions during *tracking* and *attend-RF* relative to *attend-fixation* ($p < 0.01$, paired t test) suggest that the former conditions required animals to covertly attend to the RDPs.

Finally, since we used two configurations that differed in the distance between the translating RDPs, we quantified the animals' performance in each one of them. In the far configuration, the mean distance (±std) between the patterns was larger (16.6° ± 1.2°) than in the near configuration (11° ± 4°). During both *attend-RF* and *tracking*, we found higher hit rates and lower RTs for far distances (Figures 2G and 2H). The direction of the local dots in the translating RDPs did not influence performance in any of the configurations.

Receptive Field Mapping

We recorded the responses of 157 MT neurons in the left hemisphere of both animals (88 in Se and 69 in Lu). For each unit, we first estimated the RF boundaries, the preferred (Pr), and the antipreferred (AP) motion directions at the beginning of the recording session (Khayat et al., 2010). Then we presented two "mapping" stimulus configurations of translating RDPs while the animals detected a change in the luminance of the fixation spot. In the first, the patterns' local dots moved in the cells' Pr direction. In the second, they moved in the cells' AP direction.

Figure 3A shows the responses of one example neuron to the mapping stimuli as a function of the translating RDPs position relative to an initial estimate of the RF center (dashed circle). When the RDPs' local dots moved in the Pr direction (blue), the unit responded weakly when the patterns were close to their starting and final positions, but responded more strongly when they were close to the RF center. When the translating RDPs' local dots moved in the AP direction (gray) the response was similar at all patterns' positions. These data suggest that along their trajectories the translating RDPs crossed the direction-selective unit's RF excitatory region.

In order to characterize the cell's RF profile, a Gaussian function was fitted to the responses evoked by the translating RDPs with dots moving in the unit's Pr direction. Units were classified as modulated by the RDPs position if the correlation coefficient (R) of the fit was >0.75. A total of 80 units matched this criterion (*mean R ± std* = 0.89 ± 0.05). The remaining 77 showed no response modulation by the translating RDPs position ($R < 0.75$). Responses of one of these latter units are shown in Figure 3B. Response profiles were flat ($R < 0.4$). Furthermore, responses to the Pr and AP directions of the RDPs overlapped, confirming that in these units the translating RDPs did not cross the RF excitatory region.

Neuronal Responses to the Translating-RDPs Crossing the RF

Responses of the 80 units where the translating RDPs crossed their RFs in the three main experimental conditions were recorded. Figure 4A plots the response of a unit as a function of the translating RDPs position relative to the estimated RF center (see Figure 3A). The positions of the translating RDPs (here moving in the Pr direction) are projected onto a virtual axis connecting the fixation point with the RF center. The upper two panels contain raster plots of the individual spikes in "outward" and "inward" trials (see Figure 1A), and the lower two panels show the corresponding spike density functions (SDFs). In both trial types, the cell responded vigorously to the onset of the three stimuli (response on both left and right abscissa limits). This response was likely evoked by the RF pattern since the translating RDPs were positioned outside the RF. Immediately after, the response rapidly decreased and then remained relatively constant as the translating RDPs approached the RF

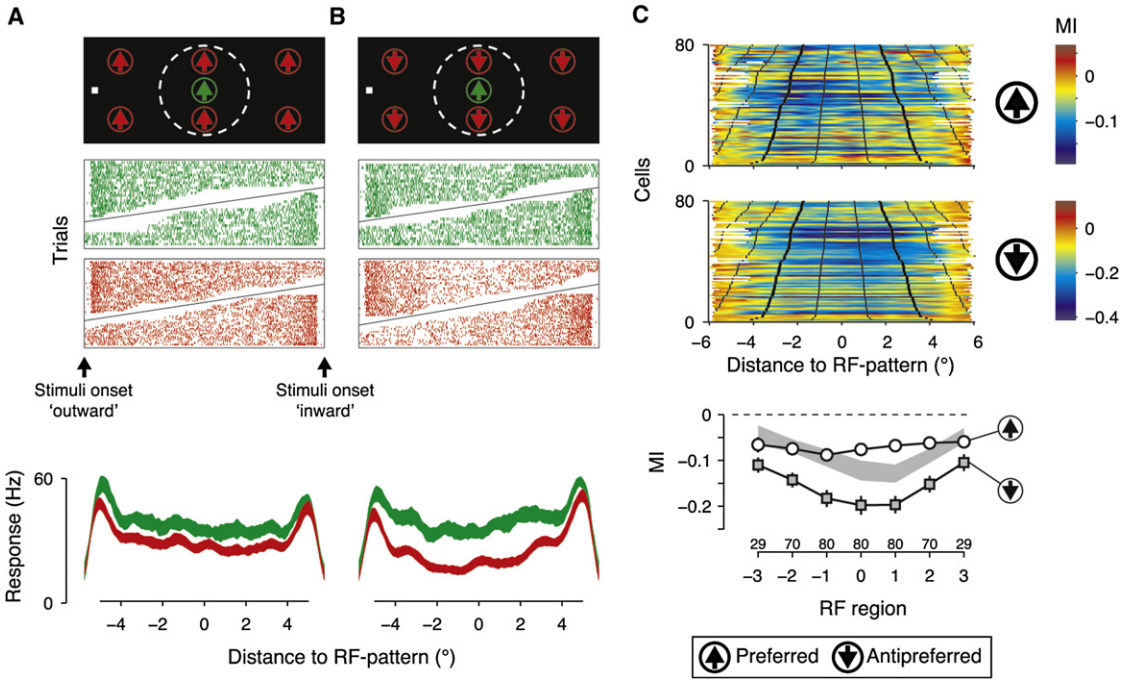

Figure 4. Response Modulation between *tracking* and *attend-RF*: Inside RF Group

(A) Cell example for the stimulus configuration with the translating RDPs dots locally moving in the Pr direction (top). Raster plots (middle) and average responses (±SEM, bottom) as a function of translating RDPs position during *attend RF* (green) and *tracking* (red).

(B) Responses of the same unit when the translating RDPs dots moved in the AP direction.

(C) Modulation indices (MIs, colors) of individual cells (ordinate) depending on the position of the Pr (top) and AP (middle) translating RDPs relative to the RF center (abscissa). Thick black lines indicate the estimated RF size and thin lines mark the RF regions over which average MIs (bottom) were computed (white circles, Pr; gray squares, AP). Error bars indicate 95% CI, and numbers above the abscissa the sample size for each RF region. The thick gray line represents the average difference (MI AP – MI Pr) ± 95% CI.

center. Interestingly, during *attend-RF* (green) responses were considerably stronger than during *tracking* (red).

When the translating RDPs' local dots moved in the AP direction (Figure 4B), the responses during *tracking* also initially increased and then continuously decreased to reach a minimum at approximately the RF center. Again, during the *attend-RF* condition responses were considerably stronger. Interestingly, the differences in response grew larger relative to Figure 4A. Thus, *tracking* decreased the responses of this unit relative to *attend-RF*, mainly when the translating RDPs were close to the RF center. This effect was stronger when the translating RDPs local dots moved in the AP direction.

We quantified these observations across all neurons by computing for each unit a modulation index (MI) between responses in both conditions (see Experimental Procedures). Positive MIs indicate higher firing rates during *tracking* relative to *attend-RF* and negative the opposite. Figure 4C shows the MIs for all neurons as a function of the translating RDPs position relative to the RF center when their dots locally moved in the Pr (top) and AP (middle) directions. Neurons were sorted according to their RF size (thick lines) and aligned to the RF center. Each RF was divided into three regions of equal size (thin black lines). To estimate the MIs along the translating RDPs trajectory these regions were extended outside the RF. For translating RDPs' with dots locally moving in the Pr direction (top) most neurons showed weaker responses during *tracking* than during *attend-RF*, with a largest difference at the RF center (blue). When dots locally moved in the AP direction (middle panel) the results were similar but the response differences were even stronger, particularly at the RF center.

To obtain a global estimate of the MIs as a function of the translating RDPs position while accounting for differences in RF size among neurons, the MIs corresponding to each region were averaged across units (Figure 4C, bottom). When the translating RDPs dots moved in the Pr direction (circles) the MIs were negative, reaching the minimum at the region immediately to the left of the RF center (abscissa = −1, $p = 0.0045$, Kruskal-Wallis ANOVA). For translating RDPs dots moving in the AP direction (squares) MIs were also negative showing even larger differences across RF regions ($p < 0.0001$, Kruskal-Wallis ANOVA). Again, this effect occurred mainly when the RDPs were aligned at the RF center (mean ± CI = −0.2 ± 0.02, 40% drop during *tracking* relative to *attend-RF*). These results show that for both configurations *tracking* decreased responses relative to *attend-RF* mainly when the RDPs were aligned close to the RF center.

We further quantified whether the modulation was stronger when the translating RDPs' dots moved in the AP direction by subtracting the MI_AP – MI_Pr for each unit and region. The mean difference across units (±95% confidence interval, gray

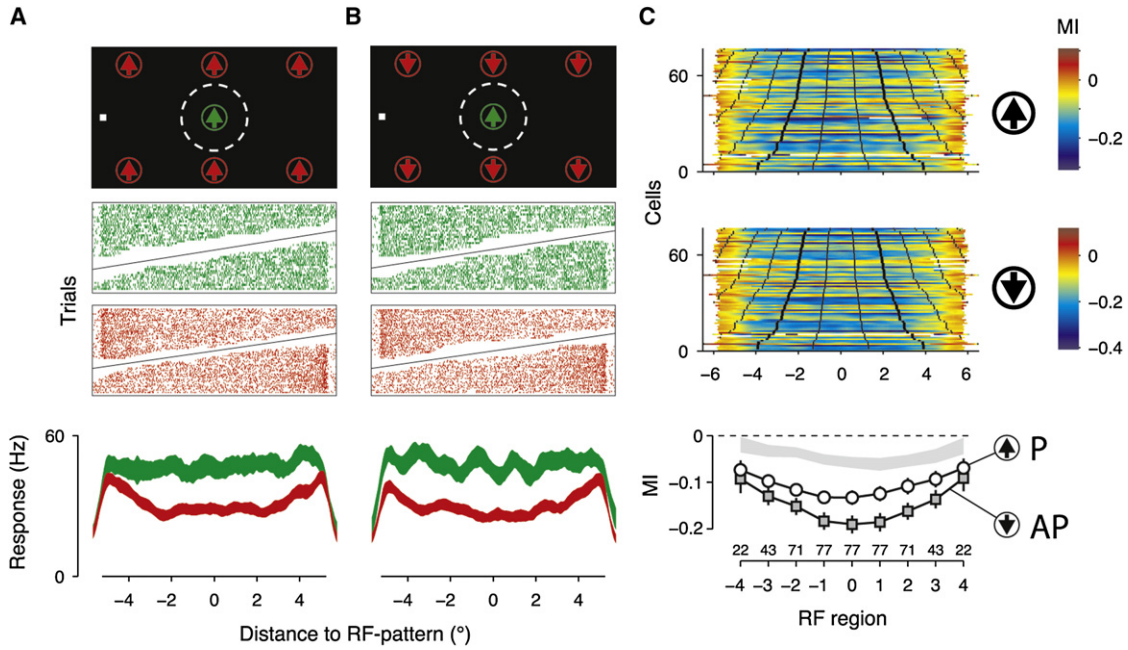

Figure 5. Response Modulation between *tracking* and *attend-RF*: Outside RF Group

(A and B) Cell example with Pr (A) and AP (B) translating RDPs.

(C) Quantification of attentional modulation using MIs.

The same conventions as in Figure 4.

line) reached its minimum at the RF center (*mean ± 95% CI at central bin* = −0.12 ± 0.02, −27% ± 4%) and became gradually smaller in the periphery ($p < 0.0001$, Kruskal-Wallis ANOVA). This shows that the modulation was stronger for the AP direction of the translating RDPs' dots.

Neuronal Responses to the Translating RDPs Circumventing the RF

We repeated a similar analysis in neurons in which the translating RDPs did not enter the RF (n = 77, Figure 3B). These units' RF size was estimated according to the distance between the RF center (considered as the center of the RF pattern) and the fixation point (see Experimental Procedures). Figure 5 shows responses of an example neuron. When the translating RDPs dots locally moved in the Pr direction (Figure 5A), responses were considerably lower during *tracking* (red) than during *attend-RF* (green). When local dots moved in the AP direction this effect was larger (Figure 5B).

At the population level (Figure 5C) responses were smaller during *tracking* than during *attend-fixation* (negative MIs in top and middle panels) reaching their strongest difference when the translating RDPs were aligned with the RF center (bottom panel, $p < 0.0001$, Kruskal-Wallis ANOVA; *mean ± CI at central bin* = −0.13 ± 0.015 for the Pr and −0.19 ± 0.019 for the AP). The differences (MI_AP − MI_Pr) reveal that the effects were larger when the translating RDPs dots locally moved in the AP direction (gray thick line). The largest difference occurred when the patterns were aligned at the RF center (mean ± 95% CI at central bin = −0.06 ± 0.01 or 11% ± 2%) and gradually decreased as the translating RDPs moved away from the RF pattern ($p = 0.0017$, Kruskal-Wallis ANOVA). Thus the response decrease during *tracking* relative to *attend-RF* also occurred when the translating RDPs circumvented the RF excitatory region.

Modulation of Neuronal Responses Relative to *attend-fixation*

The previous results may be explained by two different hypotheses. First, during *tracking* animals may have divided attention between the two translating RDPs producing a decrease of neuronal responses to the RF pattern relative to when they focused attention on the latter stimulus. Alternatively, animals may have tracked both patterns with a single large spotlight of attention and the differences in response were due to a smaller enhancement of responses to the RF stimulus when the spotlight "zoomed out" to include all patterns relative to when the spotlight was "focused" on the RF pattern (zoom lens hypothesis of Eriksen and St James, 1986).

To test the latter hypothesis, we recorded neuronal responses when animals attended to the fixation spot and ignored all the RDPs (*attend-fixation*). This condition provides an estimate of responses when no attention was devoted to the RDPs. We predict that if the animals tracked the translating RDPs with a large spotlight we should observe an increase in response relative to *attend-fixation* when translating patterns circumvented the RF. This is because during *tracking* the spotlight must unavoidably pass over the RF pattern and increase responses (Treue and Martinez-Trujillo, 1999). This prediction is more straightforward in the configuration where the translating RDPs circumvented the RF since it avoids the confounding

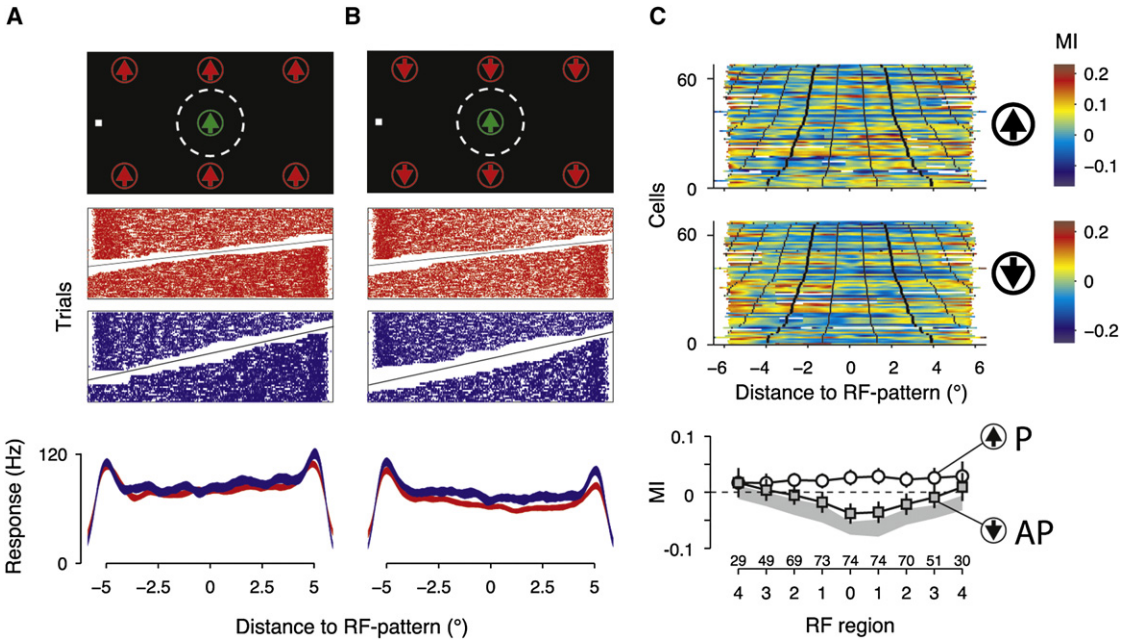

Figure 6. Response Modulation between *tracking* and *attend-fixation*: Outside RF Group

(A and B) Cell example with Pr translating (A) and AP (B) translating RDPs.

(C) Quantification of attentional modulation using MIs.

The same conventions as in Figure 4.

effect of the patterns entering the RF and modulating the cell's response.

For the example neuron in Figure 6, responses during *attend-fixation* (blue) and *tracking* (red) appear similar when the translating RDPs dots moved in the Pr direction (Figure 6A). On the other hand, for the dots' AP direction (Figure 6B) responses during *attend-fixation* are stronger than during *tracking* particularly close to the RF center. We computed MIs between responses in both conditions for 74 units (Figure 6C). Positive MIs indicate larger responses during *tracking* relative to *attend-fixation* and negative MIs the contrary. For the Pr direction of the translating RDPs responses were slightly stronger during *tracking*. However, this increase was similar along the translating RDPs trajectory ($p > 0.05$, Kruskal-Wallis ANOVA, white circles in bottom panel), suggesting that the passing of the tracked patterns alongside the RF had no effect on the responses evoked by the RF pattern. Surprisingly, for the AP direction of the translating RDPs responses were lower during *tracking* than during *attend-fixation*, particularly when the RDPs were aligned at the RF center ($p < 0.05$, Kruskal-Wallis ANOVA, squares in bottom panel). This result is inconsistent with the predictions of the zooming spotlight model since responses decreased rather than increased when the tracked patterns circumvented the RF.

We also examined the differences in response between *attend-fixation* and *attend-RF* (Figure 7). Responses in the latter condition, both at the level of single cells (Figures 7A and 7B) and the population (Figure 7C) were strongly increased relative to the former, particularly when the translating patterns circumvented the RF ($p < 0.05$, Kruskal-Wallis ANOVA, bottom panel). The effect was similar for both directions of the translating RDPs dots.

Although the different models' predictions for the neurons where the translating RDPs crossed the RF are not as clear as for the later scenario we repeated the same analysis in this dataset. The results were similar with two exceptions. There was a small increase in response during *tracking* relative to *attend-fixation* for the Pr direction of the translating RDPs dots to the right of the RF center ($p = 0.05$, Kruskal-Wallis ANOVA). Second, there was a larger increase in response for the AP direction of the translating dots in the *attend-RF* relative to *attend-fixation* (see Figure 1S). But more importantly, there was a decrease in response during *tracking* relative to *attend-fixation* when the AP translating patterns circumvented the RF suggesting that tracking decreased responses to the RF pattern. This argues against the zooming hypothesis and supports the multiple spotlights account.

Effects of Attention to Color

One remote possibility that may explain our results is that the response modulation between conditions was due to the differences in the attended stimulus color between the trial types. In our design the colors of the translating RDPs and RF pattern randomly varied from trial to trial (translating-RDPs red and RF pattern green, and vice versa). Since there were similar proportions of each color combination trials hypothetically any effects of color should have disappeared when pooling across trials. Nevertheless, we investigated this possibility by conducting a control experiment where the animals detected a change in the speed of a single RDP positioned inside the neuron's RF

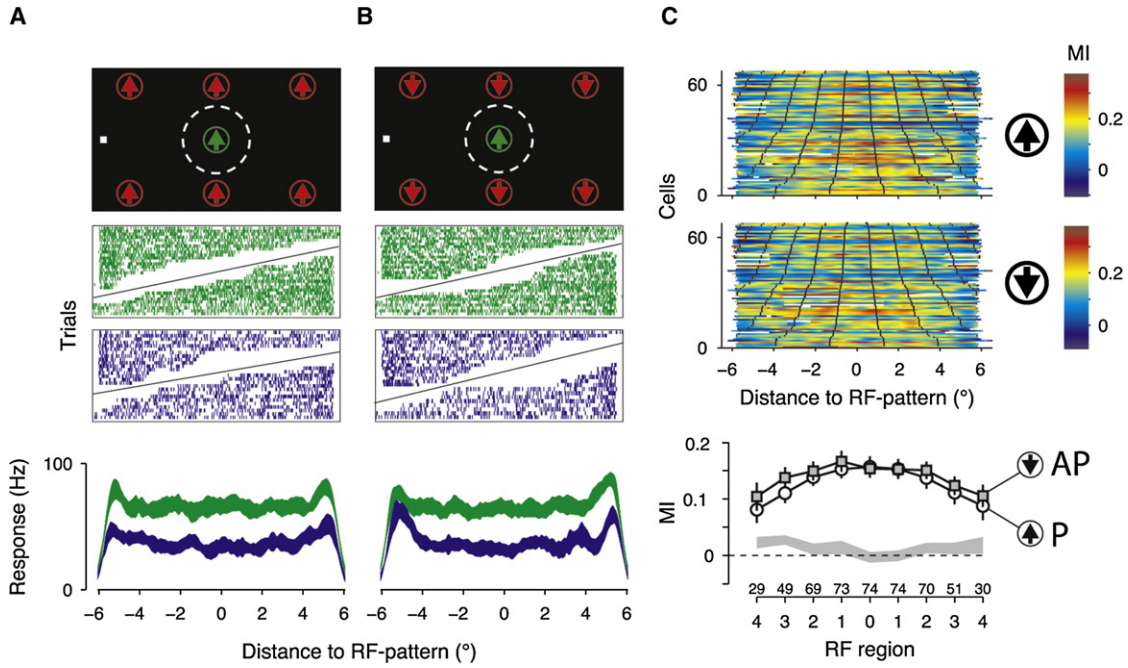

Figure 7. Response Modulation between *attend-RF* and *attend-fixation*: Outside RF Group

(A and B) Single cell example with Pr translating (A) and AP (B) translating RDPs.

(C) Quantification of attentional modulation using MIs.

The same conventions as in Figure 4.

(Figure 8). In some trials, the RDP was red while in others it was green. Across 67 units there was no difference in response between the two colors ($p > 0.79$, paired t test). Thus, attending to different colors did not modulate the responses of the recorded MT units.

Effects of Eye Position

Another possibility is that the modulation of responses, mainly between *tracking* and *attend-RF*, was due to differences in the animals' eye position between conditions. We found that the mean eye positions in both animals revealed small shifts toward the RF pattern during *tracking* relative to *attend-RF* (Figure 2S). However, the size of the shifts (0.02° and 0.14°, $p < 0.05$, paired t test) was very small relative to the neurons RF size (~5.3° in the inside group and ~4.5° in the outside group). Thus, this variable cannot account for the observed differences in response between conditions.

DISCUSSION

How the brain allocates attention to multiple stimuli has been a matter of intensive debate (see Jans et al., 2010 and Cave et al., 2010). Three main models have been proposed in which the spotlight of attention either zooms out over a region of space containing relevant objects and distracters, or switches rapidly between relevant objects, or splits into multiple foci corresponding to each relevant object and excluding distracters. We will consider the predictions of these different models in relationship to our results.

Zooming Spotlight

This model proposes that when attending to multiple objects separated by distracters the spotlight of attention zooms out including all stimuli over an entire region of the visual space (Eriksen and St James, 1986). A key model feature is that responses to all objects falling within the spotlight are enhanced; thus, in our experiment it predicts that during *tracking* responses to the irrelevant RF stimulus would be enhanced when the translating patterns circumvented but did not enter the RF. Contrary to that, we observed that when comparing the responses during *tracking* versus *attend-fixation* there was either no change in attentional modulation (Pr direction of translating RDPs) or a response decrease (AP direction) in the former relative to the latter condition.

Moreover, this model also predicts that when increasing the size of the attentional spotlight, the benefits of attention should decrease. We found, however, that performance in the far configuration was higher than that in the near configuration (Figures 2G and 2H) and the differences in attentional modulation between *tracking* and *attend-RF* were similar in both cases or even slightly larger in the far configuration (Figures 4 and 5). The performance differences between the far and near configurations during *tracking* remained when removing the RF stimulus (Figure 3S), ruling out that stronger distracter interference in the near condition was responsible for the effect. Furthermore, during a session we interleaved trials of the three different conditions to avoid that animals could predict in advance the difficulty of the upcoming trial. Animals show a higher performance in the easier tasks (i.e., *attend-fixation* and *attend-RF* showed higher

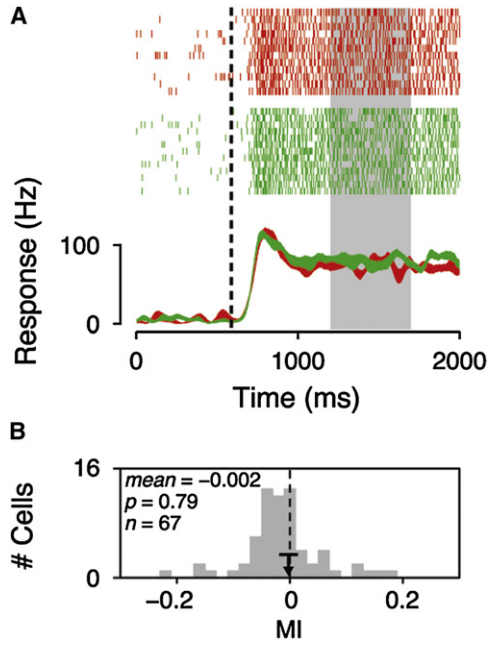

Figure 8. Attention to Color

(A) Raster plots and average spike density functions (±SEM) for RF patterns of different colors. The colors of the plots correspond to the ones of the stimuli. The gray area indicates the analysis window.

(B) MIs between the responses to the green and red RF patterns. The arrow indicates the mean MI and the horizontal bar spans the 95% CIs.

performance than *tracking*), suggesting that they could not adjust their attentional effort on a trial-by-trial basis. These findings strongly argue against the zooming spotlight hypothesis.

We consider at least two possible explanations for discrepancies between our results and those of studies providing neural correlates of the zooming model (Barriopedro and Botella, 1998; Heinze et al., 1994; McCormick and Jolicoeur, 1994; Müller et al., 2003b). First, it is possible that the coarse spatial resolution of ERPs used in those studies, does not allow measuring decreases in the activity evoked by distracters. Second, it is possible that with certain stimulus configurations and task demands the spotlight of attention zooms in/out. In fact, a recent study has provided evidence that humans can adjust the size of the attentional focus depending on task instructions (Herrmann et al., 2010).

Switching Spotlight

This model has been very difficult to test in studies of attention (Castiello and Umiltà, 1992; McCormick et al., 1998; Oksama and Hyönä, 2008; Jans et al., 2010; Cave et al., 2010). It proposes that subjects attend to multiple objects by rapidly switching a single spotlight of attention from one object to another. Testing this model's predictions against those of the split spotlight is difficult, since for very short switching times both models' predictions tend to converge. Nevertheless, our results argue against this model for the following reasons.

First, a "switching model" in which a single spotlight travels in space predicts that it should be faster to switch attention between patterns that are close together than between patterns that are farther apart. We found the opposite (Figures 2 and 3S). Second, our control experiment demonstrates an increase in RTs associated with changes in one translating RDP when its associated change probability is reduced and the change probability in the other pattern is increased. We argued that a switching spotlight should produce a RT distribution that approximates the pooled RTs distributions corresponding to both probabilities. However, we found that the pooled distribution has a higher mean than the one corresponding to 0.5-change probability targets of the main experiment. In fact, the RTs distribution corresponding to targets with the largest change probability (0.8) was similar to the one corresponding to 0.5-change probability targets. This suggest that during the main experiment the animals devoted the same amount of attention to each target as to the 0.8-target of the control experiment, and that the level of attention to any of the RDPs never decreased to values similar or close to the one corresponding to the lowest (0.2) change probability target. For a switch model to account for these data animals had to switch attention between the *50-targets* in ~12 ms or less (determined by shortening the RTs corresponding to the *20-targets* and repeating the pooling and comparison of RT distribution until it became nonsignificant). This is half of the estimated shift time from our data and much shorter than the lowest value reported for stimulus driven (35 ms) and voluntary (~200 ms) attention shifts in humans (Horowitz et al., 2009).

Third, and most importantly, we found that responses during *tracking* were decreased relative to those during *attend-RF* and *attend-fixation* when the translating stimuli circumvented the RF pattern. A switching spotlight of attention cannot account for these results. Instead, our findings suggest a relative suppression of responses to the RF pattern when it falls between the two attended RDPs. This strongly argues against models in which a single spotlight of attention travels in space, or rapidly turns on and off at the location of tracked objects (Pylyshyn and Annan, 2006).

Split Spotlight

This model proposes that when attending to multiple stimuli the spotlight of attention can split into multiple foci corresponding to each relevant stimulus and excluding distracters in between (Castiello and Umiltà, 1992; Cavanagh and Alvarez, 2005; Howe et al., 2010; Niebergall et al., 2010). The animals' behavioral performance in the main *tracking* task show that they attended to both translating RDPs. Furthermore, the results of the control experiment strongly suggest that during *tracking* the animals devoted the same amount of attention to each translating RDP while ignoring the RF pattern, and that a switching model is very unlikely to account for this result (see previous section). This conclusion is strongly supported by the decrease of responses to the RF pattern during *tracking* relative to *attend-RF* and *attend-fixation* when the three stimuli were aligned at the RF center.

We propose at least three possible explanations for the latter effect. First, splitting the spotlight of attention between the translating RDPs may increase the contribution of the suppressive surround of MT neurons (Sundberg et al., 2009) relative to the other conditions and decrease the cells' response. An argument

against this hypothesis is that MT neurons' suppressive surround is usually more strongly activated by the Pr direction (Allman et al., 1985; Bradley and Andersen, 1998; Tanaka et al., 1986; Xiao et al., 1997), but we observe the largest response decrease when the translating patterns dots moved in the AP direction. However, because the center-surround modulation could be heterogeneous and task-dependent (Huang et al., 2007, 2008), the isolated effect may be explained by interactions between these complex mechanisms and attention (Anton-Erxleben et al., 2009). This issue needs further investigation.

A second possibility is that the responses of neurons to the RF pattern were actively suppressed during *tracking* relative to *fixation* by a third inhibitory "focus" of attention covering the region in between the two attended RDPs. This result agrees with reports of a decrease in the response to one of two stimuli inside the RF of visual neurons by attention (Ghose and Maunsell, 2008; Moran and Desimone, 1985; Reynolds et al., 1999; Treue and Martínez Trujillo, 1999), as well as with changes in the spatial profile of the visual neurons' RF with attention (Ben Hamed et al., 2002; Connor et al., 1996; Womelsdorf et al., 2008).

Third, it is possible that during *tracking* the animals still allocated some attention to the RF pattern and when all RDPs where aligned they withdrew attention from that pattern causing a response decrease relative to *attend-fixation*. This explanation would agree with behavioral data showing that attentional resources could still be allocated to task-irrelevant distracters, particularly in conditions of low perceptual load (Forster and Lavie, 2008).

Feature-Based Attention

One explanation for the differences in response between *tracking* and *attend-RF* observed when the translating patterns moved in the AP direction is feature-based attention (Bichot et al., 2005; McAdams and Maunsell, 2000; Motter, 1994a; Treue and Martínez Trujillo, 1999). However, the intensity of the response modulation was largest when the translating stimuli passed across or circumvented the RF area. Feature-based attention acting alone would predict a modulation independent of the spatial position of the translating RDPs (Treue and Martínez Trujillo, 1999). Moreover, the response modulation also occurred when dots in all RDPs moved in the Pr direction. Since in both the *tracking* and *attend-RF* conditions the attended motion direction (feature) was identical feature-based attention predicts no response modulation (Martinez-Trujillo and Treue, 2004). Feature-based attention, however, may have contributed to the larger modulation observed when the translating RDPs dots moved in the AP direction since animals attended to opposite features during *tracking* and *attend-RF*.

One issue that needs clarification is the differences in the attentional modulation corresponding to the two directions of the tracking patterns (presumably due to feature-based attention) between the near and far configuration (Figures 4C and 5C). One explanation is that in the near configuration the three stimuli were aligned inside the RF, so feature-based attention may have interacted with the rules of spatial summation of responses to the various stimuli in the RF (Ghose and Maunsell, 2008). On the other hand, in the far configuration such interaction could not take place since only one stimulus was inside the RF (i.e., no spatial summation). Importantly, our results in the far configuration discard these interactions as the main source of the response modulation between the different experimental conditions.

Mechanisms of Response Modulation

One candidate mechanism for the effects isolated in our study is a differential modulation in the strength of inputs activated by attended and unattended stimuli into MT units (Ghose and Maunsell, 2008; Khayat et al., 2010; Reynolds and Heeger, 2009). During *tracking*, multifocal attention could produce an enhancement of responses in units with small RFs including the translating RDPs (e.g., in area V1), and a suppression of responses in units with RFs that included the RF pattern. Conversely, attending to the RF pattern would yield the opposite. This mechanism could be implemented in areas such as V1 or V2 where neurons are direction selective, have RFs approximately the size of the stimuli used in our study, and project toward MT (Born and Bradley, 2005; Gattass et al., 2005; Orban et al., 1986). We propose that the mechanisms of response modulation by attention depend on task conditions and their relationship with the properties of neurons within a given area (i.e., RF size and feature selectivity). Depending on the circumstances, attention may split into multiple foci, or remain as a single spotlight equivalent to the size of RFs containing individual object(s). Moreover, a single or multiple spotlight(s) of attention may also zoom in/out to match the size of the neurons' RF in a given area. Thus, at least under certain circumstances a single model may not be sufficient to characterize attention but a combination of different models may be more appropriate.

Perhaps some of the controversy in behavioral studies of attention has been motivated by the view that attention and saccades share similar neural substrates (Rizzolatti et al., 1987); i.e., because we can only saccade to one object at the time we could only attend to one object at the time. However, a powerful argument against this view is that we do not make saccades to each attended item during tasks that require monitoring several objects at the time. Moreover, it seems counterproductive, at least physiologically, to rapidly switch back and forth the spotlight of attention from one item to another. This is because the attentional modulation of responses in visual neurons does not switch on and off instantaneously but needs about 150 to 200 ms to build up (Motter, 1994b; Khayat et al., 2006; Busse et al., 2008) and produce the benefits of increased response gain and reduced variability (McAdams and Maunsell, 1999). In our task, the switch model predicts that top-down attentional signals (Moore and Armstrong, 2003) are switched on and off in the same neurons several times with a speed exceeding by far the aforementioned build-up times. Thus, a more efficient strategy would be producing a stable modulation over time in neurons with RFs containing all relevant/attended stimuli.

In sum, our results show that during tasks requiring attending to multiple objects separated by interspersed distracters attention can split into multiple spotlights corresponding to the relevant objects and filtering out interspersed distracters. This demonstrates an extraordinary adaptability of the brain's attentional mechanisms to cope with different task demands.

EXPERIMENTAL PROCEDURES

Stimuli and Task

A custom-written software running on an Apple G4 computer controlled the stimulus presentation as well as the recording of eye positions and behavioral responses. Stimuli were back-projected on a screen by a video-projector (WT610, NEC, Tokyo, Japan) at a resolution of 1,024 × 768 pixels and a refresh rate of 85 Hz. The animals sat in a primate chair in front of the screen at a viewing distance of 57 cm. The stimuli were moving random dot patterns (RDPs) composed of small bright dots (dot size = 0.01 degrees^2, dot density = 5 dots per degrees^2) moving behind circular apertures on a dark background (luminance = 0.02 cd/m^2). The dots could be either green (12.8 cd/m^2) or red (14.6 cd/m^2) and moved with 100% coherence. When they crossed one aperture's border, they were replotted at the opposite border. The diameter of each RDP was adjusted to be approximately one-third of the RF diameter.

After isolating a single neuron, we mapped its classical RF boundaries and the putative RF center (Khayat et al., 2010). During mapping the animals were rewarded for keeping gaze within a 1° fixation window at the screen center. Mapping stimuli were a bar and a RDP containing stationary dots that moved with the computer mouse. After mapping, one RDP was always positioned at the estimated RF center. The other two were positioned outside the neuron's RF at iso-eccentric locations relative to the fixation spot and RF pattern. The local motion direction and speed of dots in the RF pattern was adjusted to match the neuron's Pr direction. The local motion direction of the dots in the translating RDPs either matched the Pr or the AP direction, but it was always identical in both patterns. The local dots' speed was the same in all RDPs.

Throughout a trial, the translating RDPs followed parallel trajectories at a constant velocity of 3.5°/second, circumventing the RF pattern (Figure 1A). When the initial position of the translating RDPs was between the fixation spot and the RF pattern, they translated toward the periphery ("outward"). When their initial position was eccentric to the RF pattern, they translated toward the fixation spot ("inward"). The RDPs never overlapped. The color of both translating RDPs was always the same (red or green) but different from the RF pattern's color (green or red). The two color combinations were randomly intermixed across trials to avoid that the animals associated a color with a given stimulus type.

During trials, the animals maintained gaze on a fixation spot at the screen center and pressed a button. After 590 ms, the RF and translating patterns appeared on the screen (Figure 1A). Three different task conditions were tested. When the fixation spot color matched either that of the RF pattern (*attend-RF*), or of the translating RDPs (*tracking*), the animals had to detect a brief (110 ms) change in the corresponding pattern(s) local dots' speed (Figure 1C). The change intensity was chosen in such a way that the proportion of correct detections was 75% or higher. During *tracking*, speed changes occurred with equal probability in either one of the translating RDPs. All changes occurred at a random time between 820 and 5,060 ms from trial onset, challenging the animals to sustain attention on the target(s). Releasing the button within 150–600 ms from target change onset was rewarded with juice. We also tested the animals during a third condition in which they attended to the fixation spot and detected a change in its luminance (*attend-fixation*). The timing of these changes was similar to the one in the other two conditions. The probability that the animal obtained a hit by randomly releasing the lever between trial start and end was "450 ms / 4,020 ms = 0.106" (chance hit rate = 10.6%).

During a recording session different trial types were randomly interleaved. Approximately 30% of the trials contained a speed change in the noncued/distracter RDP(s) (e.g., in the RF pattern during *tracking*, or in one of the translating RDPs during *attend-RF*), preceding the target change. If the animal released the button in response to this speed change in a distracter, the trial was aborted without reward. This motivated the animals to attend to the target(s) and to ignore the distracter(s). Hit rate in these trials was above 94% in the *attend-RF* condition and above 90% during *tracking*. During attend-fixation the hit rate was close to 99%, significantly above chance.

Animal Preparation and Recordings

Two adult male monkeys (*Macaca mulatta*) participated in the experiments (monkey Lu weighed 5.5 kg, and monkey Se 7.2 kg). All procedures complied with the Canadian Council of Animal Care guidelines and were preapproved by the McGill University animal care committee. Titanium head posts and recording chambers (20 mm diameter, Crist Instruments, Hagerstown, MD) were surgically implanted under general anesthesia in each animal. A chamber was positioned over a craniotomy in the parietal bone giving access to the Superior Temporal Sulcus (lateral = ± 16 mm, posterior = 5 mm, aligned to interaural axis). Area MT was localized using postsurgical structural magnetic resonance imaging (MRI) (Siemens 3T Trio MR scanner) (see Khayat et al., 2010 for MRI images and stereotactic coordinates of recording sites).

Transdural penetrations were made with guide tubes using a NAN microdrive (Plexon Inc., Dallas, TX) and epoxylite insulated tungsten electrodes (FHC Inc., Bowdoin, ME; 0.125 mm shank, 1–4 MΩ impedance). Action potentials were isolated through online signal display using a Plexon system (Plexon Inc.). Spike signals were amplified and filtered (250 Hz to 10 kHz) before being digitized and stored at 40 kHz. Cells were determined to be from MT based on their response properties (selectivity, RF location and size), and the position of the electrode relative to the superior temporal sulcus (Khayat et al., 2010).

Data Analysis

In order to obtain neuronal responses with translating RDPs at different positions and at both sides of the RF, we pooled data from trials in which the RDPs translated outward and inward, but preserving the spatial relationships among the stimuli. For each trial, we computed a spike density function (SDF) by convolving each spike with a Gaussian kernel (σ = 25 ms). Trials were subsequently pooled to obtain an average SDF per condition and smoothed using a second-order "low pass" Butterworth filter with a cutoff frequency of 2.5 Hz.

Classification of Cells

We recorded responses of 157 single units in 148 recording sessions (in some sessions two units were simultaneously isolated from the same electrode). For each neuron, we determined whether the translating RDPs crossed the excitatory region of the RF by fitting Equation (1) to the average responses evoked by the RDPs as a function of the patterns' position (pos) when the animal was simply fixating the dot at the screen center (R_{avg} (pos)).

$$R_{avg}\ (pos) = R_{baseline} + R_{height} \times \exp\left(-\frac{(pos - P_{center})^2}{RF^2_{width}}\right) \quad (1)$$

The parameter $R_{baseline}$ represents the neurons firing rate when translating RDPs are outside the RF, R_{height} describes the height or gain of the response at the RF center, P_{center} represents the location of the peak response, which approximates the RF center, and RF_{width} provides an estimate of the excitatory RF region. A neuron's response was considered as modulated by the translating RDPs position when the correlation coefficient of the fit (R) was higher than 0.75, and higher than the correlation coefficient of a straight line fit with zero slope. From 157 units, 80 (*Lu:* 50; *Se:* 30) met these criteria (average R ± std = 0.88 ± 0.05). For this "inside RF" group, the distance between the translating RDPs was smaller than the RF diameter (Figure 1B, right panel), thus the patterns crossed the RF excitatory evoking a response increase (Figure 3A, blue). For the other set of neurons (n = 77; *Lu* = 38; *Se* = 39), the distance between the translating RDPs was larger than the size of the excitatory RF region (Figure 1B, right panel), thus responses did not change along the translating RDPs trajectories (outside RF group).

Attentional Modulation

The effects of attention on the neurons response were quantified by computing the following modulation index (MI):

$$MI = \frac{(R_{cond\,1} - R_{cond\,2})}{(R_{cond\,1} + R_{cond\,2})} \quad (2)$$

where R_{cond1} and R_{cond2} represent a neuron's firing rate during two experimental conditions. A positive MI indicates higher firing rates in condition 1, a negative MI higher firing rates in condition 2, and a MI of zero indicates no difference.

RF Coordinates Analysis

All the analyzed neural data were obtained from hit trials and truncated at the time of the first speed change, independently of whether the change occurred

in the target or distracter stimuli. On average, the animals correctly performed 32 ± 8 trials per stimulus configuration and condition. The number of trials with stimuli translating in opposite directions (inward and outward) was counterbalanced.

The size of MT neurons' RFs excitatory region (here referred to as the RF) can vary with eccentricity (Born and Bradley, 2005). Therefore, translating RDPs separated by the same distance might excite a neuron with a large RF but not another neuron with a small RF. Thus, before pooling data across neurons we needed to account for differences in RF size. First, we estimated the RF size for neurons in the inside RF group by using the width of the Gaussian fits (Figure 3A, gray, *mean width* ± *Std* = 5.3° ± 1.1°). For neurons in the outside RF group RF size was considered to be the RF center eccentricity multiplied by a scaling factor (Britten and Heuer, 1999; Maunsell and Van Essen, 1983; Raiguel et al., 1995).

$$RFsize = eccentricity \times 0.75. \quad (3)$$

This yielded an average RF size (±std) of 4.5° (±1.2°). This value is slightly smaller than the average RF size in the inside RF group suggesting that this group was composed of neurons with slightly smaller RFs. The RF size was divided into spatial regions (bins) over which the average MIs were computed. Each region comprised one-third of the RF size:

$$RFregion = \frac{RFsize}{3}. \quad (4)$$

This approach yielded reasonable time periods for integration of neuronal responses (mean = 464 ± 115 ms corresponding to a spatial region of ~1.6° ± 0.4°) at a resolution high enough to capture position dependent effects as the translating patterns moved through the regions. In each unit, the average MI was divided into as many regions as necessary to cover the full translating RDPs' trajectories.

Performance

For each recording session, the average percentage of correct speed change detections (hit rate) was computed. Failures to release the button within the response time window (between 150 and 600 ms after the target change onset) were considered errors. Fixation breaks were excluded from the analysis. Reaction times were defined as the duration between the onset of the target stimulus change and the button release. Analyses of performance data were conducted using nonparametric tests, and for analyzing reaction times we used parametric tests.

Eye Positions

Eye position signals were recorded using a video-based eye tracking system (Eye Link 1000, SR Research, Kanata, Ontario, Canada) with a sampling frequency of 200 Hz. Monkeys could start a trial if their eye positions were within a 1° radius from the fixation spot center. If at any time during a trial gaze position moved outside the fixation window, the trial was aborted without reward (see Khayat et al., 2010).

SUPPLEMENTAL INFORMATION

Supplemental Information includes three figures and can be found online at doi:10.1016/j.neuron.2011.10.013.

ACKNOWLEDGMENTS

This work was supported by grants to J.C.M.-T. from the Canada Research Chairs program (CRF), the Canadian Foundation for Innovation (CFI), the Canadian Institutes for Health Research (CIHR), and the EJLB foundation. P.S.K. was supported by a postdoctoral fellowship from the National Science and Engineering Research Council of Canada. S.T. and R.N. were supported by the Bernstein Center of Computational Neuroscience Göttingen (grants 01GQ0433 and 01GQ1005C), the BMBF, and the DFG Collaborative Research Center 889 "Cellular Mechanisms of Sensory Processing". R.N. was also supported by a doctoral fellowship from the DAAD.

Accepted: October 10, 2011
Published: December 21, 2011

REFERENCES

Allman, J., Miezin, F., and McGuinness, E. (1985). Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT). Perception *14*, 105–126.

Anton-Erxleben, K., Stephan, V.M., and Treue, S. (2009). Attention reshapes center-surround receptive field structure in macaque cortical area MT. Cereb. Cortex *19*, 2466–2478.

Barriopedro, M.I., and Botella, J. (1998). New evidence for the zoom lens model using the RSVP technique. Percept. Psychophys. *60*, 1406–1414.

Ben Hamed, S., Duhamel, J.R., Bremmer, F., and Graf, W. (2002). Visual receptive field modulation in the lateral intraparietal area during attentive fixation and free gaze. Cereb. Cortex *12*, 234–245.

Bichot, N.P., Rossi, A.F., and Desimone, R. (2005). Parallel and serial neural mechanisms for visual search in macaque area V4. Science *308*, 529–534.

Born, R.T., and Bradley, D.C. (2005). Structure and function of visual area MT. Annu. Rev. Neurosci. *28*, 157–189.

Bradley, D.C., and Andersen, R.A. (1998). Center-surround antagonism based on disparity in primate area MT. J. Neurosci. *18*, 7552–7565.

Britten, K.H., and Heuer, H.W. (1999). Spatial summation in the receptive fields of MT neurons. J. Neurosci. *19*, 5074–5084.

Busse, L., Katzner, S., and Treue, S. (2008). Temporal dynamics of neuronal modulation during exogenous and endogenous shifts of visual attention in macaque area MT. Proc. Natl. Acad. Sci. USA *105*, 16380–16385.

Castiello, U., and Umiltà, C. (1992). Splitting focal attention. J. Exp. Psychol. Hum. Percept. Perform. *18*, 837–848.

Cavanagh, P., and Alvarez, G.A. (2005). Tracking multiple targets with multifocal attention. Trends Cogn. Sci. (Regul. Ed.) *9*, 349–354.

Cave, K.R., Bush, W.S., and Taylor, T.G. (2010). Split attention as part of a flexible attentional system for complex scenes: comment on Jans, Peters, and De Weerd (2010). Psychol. Rev. *117*, 685–696.

Connor, C.E., Gallant, J.L., Preddie, D.C., and Van Essen, D.C. (1996). Responses in area V4 depend on the spatial relationship between stimulus and attention. J. Neurophysiol. *75*, 1306–1308.

Drew, T., McCollough, A.W., Horowitz, T.S., and Vogel, E.K. (2009). Attentional enhancement during multiple-object tracking. Psychon. Bull. Rev. *16*, 411–417.

Eriksen, C.W., and St James, J.D. (1986). Visual attention within and around the field of focal attention: a zoom lens model. Percept. Psychophys. *40*, 225–240.

Forster, S., and Lavie, N. (2008). Failures to ignore entirely irrelevant distractors: the role of load. J. Exp. Psychol. Appl. *14*, 73–83.

Gattass, R., Nascimento-Silva, S., Soares, J.G., Lima, B., Jansen, A.K., Diogo, A.C., Farias, M.F., Botelho, M.M., Mariani, O.S., Azzi, J., and Fiorani, M. (2005). Cortical visual areas in monkeys: location, topography, connections, columns, plasticity and cortical dynamics. Philos. Trans. R. Soc. Lond. B Biol. Sci. *360*, 709–731.

Ghose, G.M., and Maunsell, J.H. (2008). Spatial summation can explain the attentional modulation of neuronal responses to multiple stimuli in area V4. J. Neurosci. *28*, 5115–5126.

Heinze, H.J., Luck, S.J., Münte, T.F., Gös, A., Mangun, G.R., and Hillyard, S.A. (1994). Attention to adjacent and separate positions in space: an electrophysiological analysis. Percept. Psychophys. *56*, 42–52.

Herrmann, K., Montaser-Kouhsari, L., Carrasco, M., and Heeger, D.J. (2010). When size matters: attention affects performance by contrast or response gain. Nat. Neurosci. *13*, 1554–1559.

Horowitz, T.S., Wolfe, J.M., Alvarez, G.A., Cohen, M.A., and Kuzmova, Y.I. (2009). The speed of free will. Q J Exp Psychol (Hove) *62*, 2262–2288.

Howe, P.D., Cohen, M.A., Pinto, Y., and Horowitz, T.S. (2010). Distinguishing between parallel and serial accounts of multiple object tracking. J. Vis. *10*, 11.

Huang, X., Albright, T.D., and Stoner, G.R. (2007). Adaptive surround modulation in cortical area MT. Neuron *53*, 761–770.

Huang, X., Albright, T.D., and Stoner, G.R. (2008). Stimulus dependency and mechanisms of surround modulation in cortical area MT. J. Neurosci. *28*, 13889–13906.

Jans, B., Peters, J.C., and De Weerd, P. (2010). Visual spatial attention to multiple locations at once: the jury is still out. Psychol. Rev. *117*, 637–684.

Khayat, P.S., Spekreijse, H., and Roelfsema, P.R. (2006). Attention lights up new object representations before the old ones fade away. J. Neurosci. *26*, 138–142.

Khayat, P.S., Niebergall, R., and Martinez-Trujillo, J.C. (2010). Attention differentially modulates similar neuronal responses evoked by varying contrast and direction stimuli in area MT. J. Neurosci. *30*, 2188–2197.

Martinez-Trujillo, J.C., and Treue, S. (2004). Feature-based attention increases the selectivity of population responses in primate visual cortex. Curr. Biol. *14*, 744–751.

Maunsell, J.H., and Van Essen, D.C. (1983). Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. J. Neurophysiol. *49*, 1127–1147.

McAdams, C.J., and Maunsell, J.H. (1999). Effects of attention on the reliability of individual neurons in monkey visual cortex. Neuron *23*, 765–773.

McAdams, C.J., and Maunsell, J.H. (2000). Attention to both space and feature modulates neuronal responses in macaque area V4. J. Neurophysiol. *83*, 1751–1755.

McCormick, P.A., and Jolicoeur, P. (1994). Manipulating the shape of distance effects in visual curve tracing: further evidence for the zoom lens model. Can. J. Exp. Psychol. *48*, 1–24.

McCormick, P.A., Klein, R.M., and Johnston, S. (1998). Splitting versus sharing focal attention: comment on Castiello and Umiltà (1992). J. Exp. Psychol. Hum. Percept. Perform. *24*, 350–357.

McMains, S.A., and Somers, D.C. (2004). Multiple spotlights of attentional selection in human visual cortex. Neuron *42*, 677–686.

Moore, T., and Armstrong, K.M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. Nature *421*, 370–373.

Moran, J., and Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. Science *229*, 782–784.

Morawetz, C., Holz, P., Baudewig, J., Treue, S., and Dechent, P. (2007). Split of attentional resources in human visual cortex. Vis. Neurosci. *24*, 817–826.

Motter, B.C. (1994a). Neural correlates of attentive selection for color or luminance in extrastriate area V4. J. Neurosci. *14*, 2178–2189.

Motter, B.C. (1994b). Neural correlates of feature selective memory and pop-out in extrastriate area V4. J. Neurosci. *14*, 2190–2199.

Müller, M.M., Malinowski, P., Gruber, T., and Hillyard, S.A. (2003a). Sustained division of the attentional spotlight. Nature *424*, 309–312.

Müller, N.G., Bartelt, O.A., Donner, T.H., Villringer, A., and Brandt, S.A. (2003b). A physiological correlate of the "Zoom Lens" of visual attention. J. Neurosci. *23*, 3561–3565.

Niebergall, R., Huang, L., and Martinez-Trujillo, J.C. (2010). Similar perceptual costs for dividing attention between retina- and space-centered targets in humans. J. Vis. *10*, 4.

Oksama, L., and Hyönä, J. (2008). Dynamic binding of identity and location information: a serial model of multiple identity tracking. Cognit. Psychol. *56*, 237–283.

Orban, G.A., Kennedy, H., and Bullier, J. (1986). Velocity sensitivity and direction selectivity of neurons in areas V1 and V2 of the monkey: influence of eccentricity. J. Neurophysiol. *56*, 462–480.

Posner, M.I., Snyder, C.R., and Davidson, B.J. (1980). Attention and the detection of signals. J. Exp. Psychol. *109*, 160–174.

Pylyshyn, Z.W., and Annan, V., Jr. (2006). Dynamics of target selection in multiple object tracking (MOT). Spat. Vis. *19*, 485–504.

Raiguel, S., Van Hulle, M.M., Xiao, D.K., Marcar, V.L., and Orban, G.A. (1995). Shape and spatial distribution of receptive fields and antagonistic motion surrounds in the middle temporal area (V5) of the macaque. Eur. J. Neurosci. *7*, 2064–2082.

Reynolds, J.H., and Heeger, D.J. (2009). The normalization model of attention. Neuron *61*, 168–185.

Reynolds, J.H., Chelazzi, L., and Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. J. Neurosci. *19*, 1736–1753.

Rizzolatti, G., Riggio, L., Dascola, I., and Umiltá, C. (1987). Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. Neuropsychologia *25* (1A), 31–40.

Sundberg, K.A., Mitchell, J.F., and Reynolds, J.H. (2009). Spatial attention modulates center-surround interactions in macaque visual area v4. Neuron *61*, 952–963.

Tanaka, K., Hikosaka, K., Saito, H., Yukie, M., Fukada, Y., and Iwai, E. (1986). Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. J. Neurosci. *6*, 134–144.

Treue, S., and Martínez Trujillo, J.C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. Nature *399*, 575–579.

Womelsdorf, T., Anton-Erxleben, K., and Treue, S. (2008). Receptive field shift and shrinkage in macaque middle temporal area through attentional gain modulation. J. Neurosci. *28*, 8934–8944.

Xiao, D.K., Raiguel, S., Marcar, V., and Orban, G.A. (1997). The spatial distribution of the antagonistic surround of MT/V5 neurons. Cereb. Cortex *7*, 662–677.