

# Dynamic shifts of visual receptive fields in cortical area MT by spatial attention

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Voluntary attention is the top-down selection process that focuses cortical processing resources on the most relevant sensory information. Spatial attention—that is, selection based on stimulus position—alters neuronal responsiveness throughout primate visual cortex. It has been hypothesized that it also changes receptive field profiles by shifting their centers toward attended locations and by shrinking them around attended stimuli. Here we examined, at high resolution, receptive fields in cortical area MT of rhesus macaque monkeys when their attention was directed to different locations within and outside these receptive fields. We found a shift of receptive fields, even far from the current location of attention, accompanied by a small amount of shrinkage. Thus, already in early extrastriate cortex, receptive fields are not static entities but are highly modifiable, enabling the dynamic allocation of processing resources to attended locations and supporting enhanced perception within the focus of attention by effectively increasing the local cortical magnification.

Vision at an attended location is faster, more accurate, and of higher spatial resolution and enhanced sensitivity for fine changes<sup>1–4</sup>. Stimuli outside this ‘spotlight of attention’ appear to have lower contrast or might not be perceived at all<sup>5,6</sup>. Physiologically, one well-investigated effect of attention in visual cortex is a multiplicative modulation of neuronal responses<sup>7–9</sup>. But not all observed effects of attentional modulation are clearly multiplicative<sup>10–11</sup>. Most prominently, this is the case for the effect observed when one of two stimuli inside the receptive field is attended to: attending to the stimulus that elicits the stronger sensory response when presented alone typically enhances responses, whereas attending to the less optimal stimulus reduces responses<sup>12–14</sup>. It has been suggested<sup>12</sup> that the neural basis of this differential, push-pull modulation of the respective effectiveness of each stimulus is a shrinkage of receptive fields around the attended stimuli. This would attenuate the influence of unattended stimuli at nearby locations. This influential hypothesis has never been empirically validated. Such changes in the profiles of receptive fields would have far-reaching consequences in successive areas of the cortical processing hierarchy<sup>15–18</sup>. In particular, it would provide higher-order areas with an almost exclusive representation of stimuli at the attended spatial location<sup>19</sup>.

## RESULTS

### Neuronal shifts with attention inside the receptive field

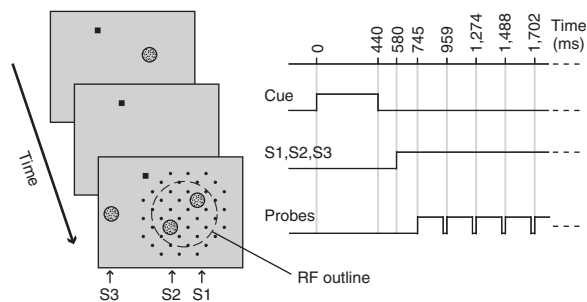
To investigate the influence of attention on receptive fields, we recorded from 78 neurons in cortical area MT of two macaque monkeys. Area MT is an early processing stage in the dorsal pathway and is central for the processing of visual motion information. Recordings were made while the monkeys’ attention was directed to one of two stimuli (S1, S2)

moving in the antipreferred direction inside the receptive field, or to a third stimulus (S3) positioned outside the receptive field (Fig. 1). We acquired high-resolution maps of a neuron’s receptive field by presenting a succession of brief probe stimuli at up to 52 positions covering the receptive field (sparing the locations of S1 and S2) while the monkey’s attention was allocated to one of the three stimuli. Probe stimuli were of the same size as S1, S2 and S3 but of higher contrast, and they moved in the preferred direction of the neuron. We conjectured that the hypothesized distortion of the receptive field would result in a push-pull effect, enhancing probe responses around the attended location and reducing responses to the probe farther from this focus of attention.

The results for an example neuron (Fig. 2; see also **Supplementary Fig. 1** online) illustrate that the most responsive part of the receptive field was shifted substantially toward the attended position inside the receptive field (that is, when attention was directed toward S1 and S2, which were located inside the receptive field). To quantify this effect across our sample of 78 MT neurons, we determined the ‘neuronal shift’: the amount by which the center of mass of each receptive field shifted between the conditions when attention was directed to S1 versus S2 along the axis of the ‘attentional shift’ (that is, the connection between the locations of S1 and S2). Positive values indicated shifts in the same direction as the attentional shift (that is, toward the focus of attention; Fig. 3a). Across our cells, we found a highly significant neuronal shift that averaged 30.3% of the attentional shift (Fig. 3b horizontal axis,  $P < 0.001$ ,  $t = 14.0$ , one-sample  $t$ -test). For the sample of receptive field sizes and stimulus locations in our study, this corresponded to an average shift of  $3.0^\circ$  of visual angle or 22% of the receptive field diameter. Additionally, we determined the shift for the orthogonal direction (with positive values indicating shifts toward the

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**Figure 1** Experimental protocol. Time course of events and example of the placement of cue, stimuli and probes in an experimental trial (details in Methods). Black square, fixation point.

fovea) as a measure of the variability of the data. This distribution showed no significant bias (Fig. 3b vertical axis,  $P = 0.48$ ).

To determine how many of the individual cells showed a significant shift, we performed a bootstrap analysis (Supplementary Note online). Of our 78 cells, 49 (63%) showed a significant ( $P < 0.05$ ) receptive field shift in the direction of the attentional shift, and none shifted significantly in the opposite direction. In contrast, the orthogonal shift was significant ( $P < 0.05$ ) in only 3 cells (3.8%), indicating that the receptive fields displacement fell along the axis of the attentional shift.

We can rule out the possibility that the neuronal shift was due to small differences in eye position across conditions, because we calculated the deviation in eye position along the axis of the attentional shift and found an average displacement of only  $0.0182^\circ (\pm 0.0065^\circ, \text{s.e.m.})$ ; details in Supplementary Note and Supplementary Fig. 2 online).

### Receptive field size changes with attention

To determine if the neuronal shift was accompanied by the hypothesized shrinkage of the receptive field around the attended stimulus, we compared the size of receptive fields when attention was directed inside versus outside the receptive field. Whereas receptive fields were, on average, 4.3% smaller with attention inside the receptive field (Fig. 3c), this effect was only marginally significant ( $\pm 3.4\%$ , 95% confidence interval,  $P < 0.05$ ,  $t = -2.56$ , paired  $t$ -test). Receptive field shrinkage was isotropic—that is, similar in magnitude parallel and orthogonal to the direction of the attention shift (Supplementary Note and

Supplementary Fig. 3 online). Thus, the influence of spatial attention was dominated by a shift, rather than a shrinkage, of receptive fields, and our observation of only a small amount of shrinkage resonates with the psychophysical observation of a coarse spatial resolution of visual attention<sup>20</sup>.

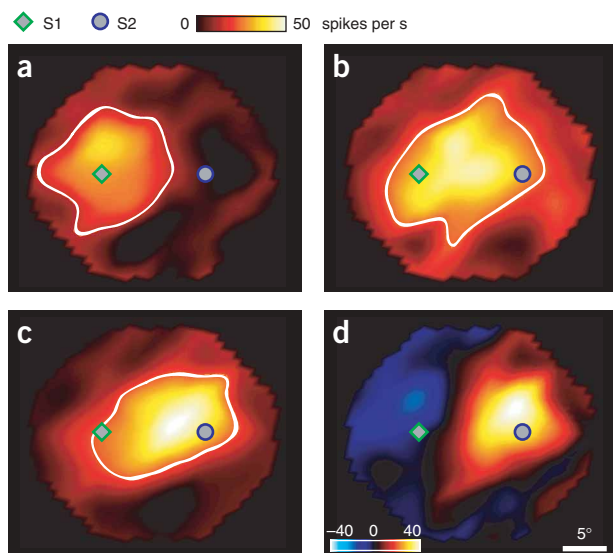
Our findings demonstrate that the enhanced/reduced response of MT neurons when spatial attention is directed to the preferred/antipreferred of two stimuli inside their receptive field can be accounted for by a systematic and large change in the receptive field profile. In effect, attention changes the spatial filtering characteristics of those MT neurons whose receptive fields overlap with the currently attended location.

### Spatial extent of receptive field shifts with attention

For an attentional location just outside the receptive field, a previous study in area V4 (ref. 21) has demonstrated that receptive fields are distorted toward the location of attention. We were wondering if such an effect is also present in area MT and if it extends beyond the immediate surround of the receptive field. To investigate this issue, we compared the receptive field profile when attention was directed to either S1 or S2, located inside the receptive field (the ‘in’ condition), to the profile when attention was directed to S3, located far outside the receptive field in the opposite hemifield (the ‘out’ condition; Fig. 4a). If the receptive field in the out condition was unaffected by the location of the attentional focus relative to the receptive field, the in condition should shift the receptive field center along a vector pointing directly at the attended stimulus’ location inside the receptive field. If, on the other hand, the receptive field center in the out condition was already attracted toward the attended stimulus’ location outside the receptive field, then switching to the in condition should not only shift the center to the new location of attention, but should also release it from the attraction toward the S3 location. In this case, the resulting shift vector should not point directly at the attended stimulus’ location inside the receptive field, but should be deviated somewhat by a vector component pointing away from the direction of S3. We found just that for a significant majority of the vectors (62.5%,  $P < 0.05$ , Wilcoxon signed rank test; Fig. 4b). Further support for a shift of the receptive field center toward the location of attention in the out condition came from the finding that the eccentricities of the receptive fields in trials with attention outside the receptive field were smaller than their eccentricities in trials with attention inside the receptive field (7.9%,  $P = 0.019$ , paired  $t$ -test). These findings are not only in agreement with the findings from V4, but go well beyond them in demonstrating a far-reaching effect of spatial attention that even affects neurons with receptive fields in the opposite hemifield.

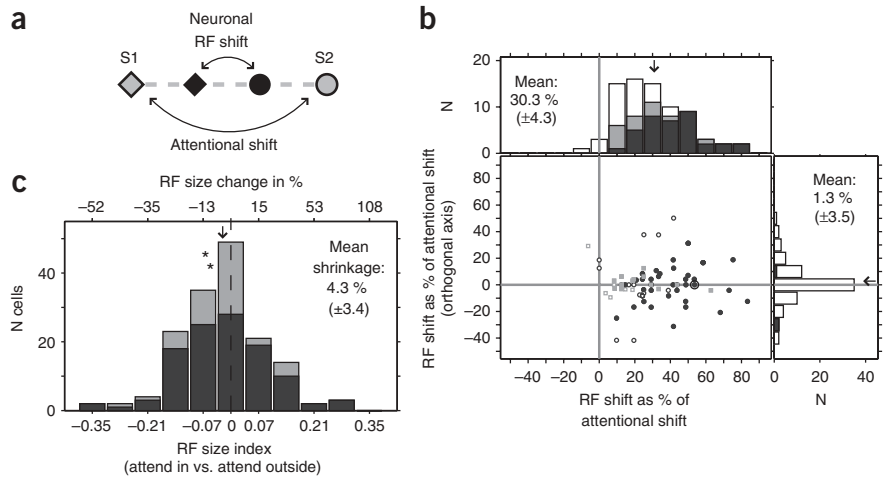
### DISCUSSION

One effect of spatial attention that has been reported frequently is a multiplicative modulation of tuning curves<sup>7–9</sup>. The push-pull modulation of MT receptive fields with shifts of spatial attention within the



**Figure 2** Receptive field profiles of an example cell, as 2D surface plots. (a–c) Receptive field (RF) profiles when attention was directed inside the RF, to stimulus S1 (a) or S2 (c), or when attention was directed outside the RF, to S3 (b). The surface color at each point in the plots indicates the increase in the neuron’s response elicited by the presentation of a probe stimulus at that position, over the response observed in the absence of a probe (that is, when only S1 and S2 were present). Supplementary Fig. 1 online shows the same data as absolute firing rates. (d) Difference map, computed by subtracting the RF when attention was on S1 from the RF when attention was on S2. The map illustrates that shifting attention from S1 to S2 enhances responsiveness around S2 and reduces it near S1.

**Figure 3** Quantification of RF shift and shrinkage. (a) Convention used to quantify the shift of RF centers. (b) Magnitudes of the neural shifts, along the axis of the attentional shift (x-axis and top histogram) or orthogonal to it (y-axis and right histogram; positive values indicate shifts toward the fovea). Light gray, monkey D; dark gray, monkey R. Circle, example cell illustrated in **Figure 2** (attentional shift: +53.6%). Filled and unfilled histogram bars and symbols indicate significant ( $P < 0.05$ ) and nonsignificant shifts, respectively. The top histogram shows a highly significant mean neuronal shift toward the attended stimulus ( $30.3\% \pm 4.3\%$  (95% CI),  $P < 0.001$ ). This mean shift was larger in monkey R ( $35\% \pm 4.8\%$ ) than in monkey D ( $18\% \pm 6.2\%$ ). There was no significant bias in the direction orthogonal to the direction of the attentional shift (mean:  $1.3\% \pm 3.5\%$ ). (c) Histogram of RF size changes when attention was directed outside versus inside the RF. Stars, size change of the example cell from **Figure 2**; the RF shrank when attention was directed toward S1 or S2 ( $-9.5\%$  and  $-4.4\%$ , respectively). The histogram is shifted slightly to the left, indicating a small but significant mean reduction of RF size ( $4.3 \pm 3.4\%$ , 95% CI,  $P < 0.05$ , paired *t*-test) when attention was directed into the RF. The size reduction did not differ significantly between the two monkeys and was around the 0.05 significance level when the two data sets were analyzed separately (monkey R:  $-3.7\% \pm 4.3\%$ ,  $P = 0.077$ ; monkey D:  $-5.7\% \pm 5.6\%$ ,  $P = 0.039$ ).



receptive field is not a multiplicative change of a neuron's spatial tuning curve; nevertheless, it is important to point out that the underlying attentional modulation might still be multiplicative. If attention differentially acts on the neurons with smaller receptive fields that provide the input to MT, the observed modulation in receptive field profiles could be achieved with multiplicative effects: for instance, by increasing the response gain of input neurons representing the attended location and decreasing the response gain of the neurons representing unattended regions within the MT receptive field<sup>15</sup>.

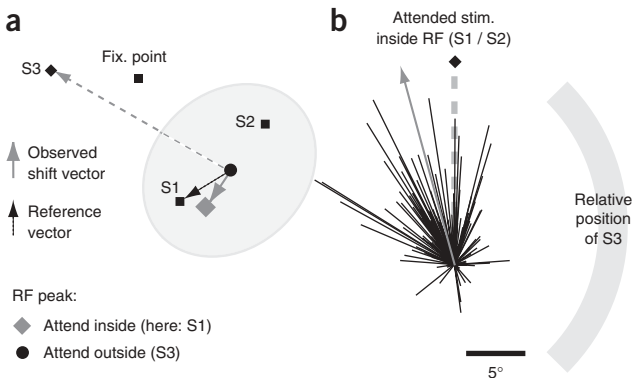
Our findings show that spatial attention shifts the receptive fields of MT neurons toward the attentional focus. Such a dynamic routing provides a powerful mechanism to increase selectivity of visual representations within and across functionally specialized visual areas, and serves to constrain models of the perceptual organization of selective visual processing. For the neural population as a whole, the spatial shift reflects the additional recruitment of processing resources at the focus of attention. Paralleling the increase in the observed magnitude of attentional modulation, the shifts of receptive fields probably increase with increasing receptive field size in successive areas of the visual hierarchy. It could also be the neural correlate of various perceptual effects that are centered on the focus of attention, including enhanced processing accuracy and spatial resolution close to the attentional focus, suppression in its surround and distortions in spatial judgments<sup>22–25</sup>.

In summary, our finding that receptive fields are highly malleable by the attentional state demonstrates a dynamic spatial filtering system that could provide the neuronal correlate of the central purpose of attentional modulation: namely, the allocation of processing resources to the attended stimuli at the expense of the unattended ones. This dynamic modification by spatial attention seems to affect the receptive field mosaic across the whole visual field and is likely to be part of a mechanism active during the planning or execution of eye movements<sup>26–29</sup>. Furthermore, the similarity between the far-reaching influence of spatial attention across the visual field and the distribution of feature-based attention<sup>7</sup> supports the hypothesis that both rely on a common underlying mechanism.

**METHODS**

**Electrophysiological recording.** All procedures reported in this study were approved by the district government of Braunschweig, Lower Saxony, Germany. Neuronal activity was recorded from 57 and 21 single isolated cells from

**Figure 4** Receptive field shift when attention is directed inside versus outside the receptive field. (a) Typical stimulus arrangement. Black circle and gray diamond, RF center positions. Vectors indicate the direction of a direct shift of the RF center toward the attended stimulus inside the RF (the 'reference vector') and the direction of the observed shift. Note that the eccentricity of the RF when attention was directed inside the RF (distance from fixation point to gray square) was, on average, 7.9% larger than the RF eccentricity when attention was directed to S3 (distance from fixation point to black circle). We analyzed the data from the two monkeys separately and found that this effect was significant only in monkey R ( $9.9\%$ ,  $P = 0.02$ ). (b) Distribution of observed shift vectors. These data are based on the 64 cells for which sufficient data were available for both the attend-outside (to stimulus S3) and each of the attend-inside (to stimulus S1 or S2) conditions. All vectors were rotated, such that the reference vector would point straight up, and flipped horizontally (if necessary), such that the S3 stimulus position would be on the right. The gray arrow pointing in the direction opposite to the location of S3 indicates a systematic and significant deviation of the vectors (average deviation of  $15.2^\circ$ , 95% angular confidence:  $\pm 9.8^\circ$ ,  $P < 0.05$ ), and implies a far-reaching modulation of receptive fields by attention. We analyzed the data from the two monkeys separately and found that this effect was significant only in monkey R ( $19.2 \pm 10.5^\circ$ ,  $P < 0.05$ ).



monkeys R and D, respectively, with tungsten electrodes (impedance 1.0–4.0 M $\Omega$ , Frederick Haer). Cell isolation was based on window discrimination (BAK Electronics or Plexon). Cells were localized in area MT by their physiological characteristics and the histological reconstruction of recording sites in monkey R. Access to MT was provided by a craniotomy and a recording chamber surgically implanted above the superior temporal sulcus of the left hemisphere. During the experiment, a custom computer program running on an Apple Macintosh PowerPC controlled stimulus presentation, and monitored and recorded eye positions and neuronal and behavioral responses. Eye positions were determined using a high-resolution, video-based eye tracking system (ET49, Thomas Recording GmbH) with a sampling frequency of 230 Hz, and were digitized and stored at 200 Hz.

**Visual stimuli.** Stimuli were moving random dot patterns (RDPs) of small bright dots (density: 10 dots per deg<sup>2</sup>) plotted within a stationary circular aperture on a dark (0.7 cd) computer monitor. For each receptive field, stimuli S1 and S2 were placed at similarly responsive positions in the receptive field at equal eccentricity and equidistant from the center of the receptive field when the monkey was directing its attention to the fixation point. S3 was placed in the opposite hemifield. Initial estimation of this ‘sensory’ receptive field center was based on a manual mapping with a mouse-controlled RDP and with quantitative mapping during the main experiment. Note that the shift and shrinkage of the receptive field when attention was directed to S1 or S2 could cause the other stimulus to fall outside the receptive field on those trials (see Fig. 2a–c for an example). Note also that the initial manual mapping was used only for the placement of the stimuli. All receptive fields profiles used in the analysis were mapped quantitatively during temporally interleaved trials in which attention was directed to S1, S2, S3 or the fixation point. Therefore all receptive field profiles used in the analysis were determined with temporally interleaved mapping. This ensured that the results were not contaminated by potential changes in a neuron’s isolation or responsiveness over time.

Stimuli S1, S2 and S3 moved in the cell’s antipreferred direction and with a reduced luminance (19 cd) in order to prevent a saturation of the cell’s response due to the presence of S1 and S2 alone. A fourth RDP (the ‘probe’, 47 cd) moving in the preferred direction of the neuron was used to probe the spatial sensitivity. This probe stimulus was of the same size as S1, S2, and S3, and was presented at the intersections of a dense grid (between 42 and 52 positions) spanning the classical receptive field and its immediate surround, but sparing the S1 and S2 location (in order to avoid potential nonlinear interactions and changes in the sensory quality of S1 and S2 that could affect the attentional task performed on these stimuli). The longer axis of the elliptical probe grid was always along the S1–S2 axis.

**Experimental procedure.** First we isolated a single cell and determined its preferred direction. Then we centered the virtual grid of the array of probe positions at the estimated center of the receptive field (Fig. 1), in an approach similar to that used in a previous study<sup>30</sup>. A trial started once the monkey’s gaze was directed within 0.75° of the fixation point. After the monkey touched a lever, the cue (a stationary RDP) appeared for 445 ms at the upcoming position of either S1, S2 or S3, indicating the ‘target’ location for the trial. After a 145-ms interstimulus interval, S1, S2 and S3 were presented. The task was to detect a brief (80 ms) phase during which the target (the stimulus at the previously cued location) moved in a different direction, while ignoring equivalent phases in the two other RDPs (the ‘distracters’). Successive presentation of the receptive field probe stimulus began 160 ms after the onset of S1, S2 and S3. Probe duration was 187 ms with an interprobe blank period of 27 ms. The direction of the target and the distracter stimuli changed 670–4,670 ms after the trial began; the times of these changes were randomly picked from a uniform distribution. In control trials, the monkey had to detect a change in the color of the fixation square. Trials were aborted if the monkey’s gaze left the fixation window or if the monkey released the lever outside a 150- to 750-ms time window after the change of the target stimulus (for example, because the monkey released the lever in response to a distracter change, or if it failed to detect the target change).

**Data analysis.** To analyze the data, we used the mean neuronal responses to probe presentations from only the correctly completed trials in the three experimental conditions (that is, when attention was directed to S1 (‘attend-

inside’ receptive field), to S2 (‘attend-inside’ receptive field) or to S3 (‘attend-outside’ receptive field)). The mean firing rate was computed for a 60- to 200-ms interval after the onset of the probe stimulus. For each condition, some of the probe presentations were skipped (that is, no probe was shown) in order to determine the cell’s response to S1 and S2 alone. This baseline was subtracted from all probe responses before the interpolation of the receptive field profile by cubic spline interpolation. These two-dimensional (2D) profiles were used to determine receptive field centers and sizes.

We calculated the shift of the receptive field (Fig. 3b) between attentional conditions by using the center of mass of one-dimensional projections of the receptive field surface. For this analysis, we averaged the activity of the receptive field profile orthogonal to the axis connecting the two stimuli within the receptive field (Fig. 3b, horizontal axis) or to an orthogonal axis (Fig. 3b, vertical axis). Averaging was limited to regions of the receptive field surface that exceeded two s.d. of the baseline response in any of the attentional conditions, in order to exclude visual field regions that did not contribute to the receptive field profile. For each 2D projected receptive field slice, we determined the center of mass and the peak positions (data not shown but qualitatively identical to results with the center of mass). Receptive field shifts between the two attend-inside conditions are expressed as the proportional distance of the center of mass relative to the reference distance between the stimuli S1 and S2 (Fig. 3a). Shift values were positive when the receptive field center lay closer to the attended stimulus in the respective attentional conditions.

To quantify the statistical significance of the shift of the neuronal receptive fields for individual cells, we applied a bootstrap method (details in **Supplementary Note**).

The receptive field size was calculated as the square root of the area in which the 2D receptive field surface exceeded the half-maximal response (after subtracting the baseline responses—that is, responses in the same attentional condition when S1 and S2 were present but no probe stimulus was shown). We compared receptive field sizes when attention was directed to the stimulus outside the receptive field versus when attention was directed to either of the stimuli inside the receptive field, by using an attentional modulation index<sup>13</sup>:  $(S_{in} - S_{out}) / (S_{in} + S_{out})$ , where  $S_{in}$  and  $S_{out}$  are the size of the receptive field when attention was directed inside and outside, respectively. The size index ranges between –1 and 1; negative values reflect a smaller receptive field size when attention was directed inside the receptive field compared to outside the receptive field (Fig. 3c). The average index value is a conservative estimate as it corresponds to a geometric mean (that is, the mean is less influenced by large values than a regular mean would be).

*Note: Supplementary information is available on the Nature Neuroscience website.*

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#### AUTHOR CONTRIBUTIONS

T.W. and S.T. conceived the experiment and performed the data analysis. T.W. and K.A.-E. performed the experiments. F.P. provided technical assistance and helped during the experiment. T.W. and S.T. wrote the paper.

#### COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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1. Yeshurun, Y. & Carrasco, M. Attention improves or impairs visual performance by enhancing spatial resolution. *Nature* **396**, 72–75 (1998).
2. He, S., Cavanagh, P. & Intriligator, J. Attentional resolution and the locus of visual awareness. *Nature* **383**, 334–337 (1996).
3. Hawkins, H.L. *et al.* Visual attention modulates signal detectability. *J. Exp. Psychol. Hum. Percept. Perform.* **16**, 802–811 (1990).

4. Carrasco, M., Williams, P.E. & Yeshurun, Y. Covert attention increases spatial resolution with or without masks: support for signal enhancement. *J. Vis.* **2**, 467–479 (2002).
5. Carrasco, M., Ling, S. & Read, S. Attention alters appearance. *Nat. Neurosci.* **7**, 308–313 (2004).
6. Simons, D.J. & Rensink, R.A. Change blindness: past, present, and future. *Trends Cogn. Sci.* **9**, 16–20 (2005).
7. Treue, S. & Martinez Trujillo, J.C. Feature-based attention influences motion processing gain in macaque visual cortex. *Nature* **399**, 575–579 (1999).
8. McAdams, C.J. & Maunsell, J.H. Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. *J. Neurosci.* **19**, 431–441 (1999).
9. Martinez-Trujillo, J.C. & Treue, S. Feature-based attention increases the selectivity of population responses in primate visual cortex. *Curr. Biol.* **14**, 744–751 (2004).
10. Reynolds, J.H. & Chelazzi, L. Attentional modulation of visual processing. *Annu. Rev. Neurosci.* **27**, 611–647 (2004).
11. Treue, S. Neural correlates of attention in primate visual cortex. *Trends Neurosci.* **24**, 295–300 (2001).
12. Moran, J. & Desimone, R. Selective attention gates visual processing in the extrastriate cortex. *Science* **229**, 782–784 (1985).
13. Treue, S. & Maunsell, J.H. Effects of attention on the processing of motion in macaque middle temporal and medial superior temporal visual cortical areas. *J. Neurosci.* **19**, 7591–7602 (1999).
14. Reynolds, J.H., Chelazzi, L. & Desimone, R. Competitive mechanisms subserve attention in macaque areas V2 and V4. *J. Neurosci.* **19**, 1736–1753 (1999).
15. Maunsell, J.H.R. & McAdams, C.J. Effects of attention on the responsiveness and selectivity of individual neurons in visual cerebral cortex. in *Visual Attention and Cortical Circuits* (eds. Braun, J., Koch, C. & Davis, J.L.) Ch. 6 103–120 (MIT Press, Cambridge, Massachusetts, 2001).
16. Reynolds, J.H. & Desimone, R. The role of neural mechanisms of attention in solving the binding problem. *Neuron* **24**, 19–29 (1999).
17. Salinas, E. & Abbott, L.F. A model of multiplicative neural responses in parietal cortex. *Proc. Natl. Acad. Sci. USA* **93**, 11956–11961 (1996).
18. Itti, L. & Koch, C. Computational modelling of visual attention. *Nat. Rev. Neurosci.* **2**, 194–203 (2001).
19. Everling, S., Tinsley, C., Gaffan, D. & Duncan, J. Filtering of neural signals by focused attention in the monkey prefrontal cortex. *Nat. Neurosci.* **5**, 671–676 (2002).
20. Intriligator, J. & Cavanagh, P. The spatial resolution of visual attention. *Cognit. Psychol.* **43**, 171–216 (2001).
21. Connor, C.E., Preddie, D.C., Gallant, J.L. & Van Essen, D.C. Spatial attention effects in macaque area V4. *J. Neurosci.* **17**, 3201–3214 (1997).
22. Suzuki, S. & Cavanagh, P. Focussed attention distorts visual space: an attentional repulsion effect. *J. Exp. Psychol. Hum. Percept. Perform.* **23**, 443–463 (1997).
23. LaBerge, D., Carlson, R.L., Williams, J.K. & Bunney, B.G. Shifting attention in visual space: tests of moving-spotlight models versus an activity-distribution model. *J. Exp. Psychol. Hum. Percept. Perform.* **23**, 1380–1392 (1997).
24. Müsseler, J., Stork, S. & Kerzel, D. Comparing mislocalizations with moving stimuli. The Fröhlich effect, the flash-lag effect and representational momentum. *Vis. cogn.* **9**, 120–138 (2002).
25. Tsai, Y. & Bareket, T. Effects of attention on localization of stimuli in the visual field. *Psychon. Bull. Rev.* **6**, 292–296 (1999).
26. Ben Hamed, S., Duhamel, J.R., Bremmer, F. & Graf, W. Visual receptive field modulation in the lateral intraparietal area during attentive fixation and free gaze. *Cereb. Cortex* **12**, 234–245 (2002).
27. Duhamel, J.R., Colby, C.L. & Goldberg, M.E. The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* **255**, 90–92 (1992).
28. Tolia, A.S. *et al.* Eye movements modulate visual receptive fields of V4 neurons. *Neuron* **29**, 757–767 (2001).
29. Krekelberg, B., Kubischik, M., Hoffmann, K.P. & Bremmer, F. Neural correlates of visual localisation and perisaccadic mislocalisation. *Neuron* **37**, 537–545 (2003).
30. Britten, K.H. & Heuer, H.W. Spatial summation in the receptive fields of MT neurons. *J. Neurosci.* **19**, 5074–5084 (1999).