Supplementary information: Attention alters spatial integration in Macaque V1 in an eccentricity dependent manner

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Supplementary information 1: Do contrast sensitivity, spatial frequency preference, and receptive field size determine the influence of attention on neuronal length preference?

It could be argued that differences in contrast sensitivity, RF size, or spatial frequency tuning are responsible for the different effects of attention on length tuning, rather than eccentricity per se. To investigate this possibility we have analysed how each of these parameters influences the effect of attention on length tuning. We will first report on the findings in relation to contrast sensitivity, then in relation to spatial frequency tuning, then in relation to receptive field size.

Contrast sensitivity:

We recorded contrast sensitivity from a total of 56 cells, from which we also recorded the preferred length in relation to attention. Contrast sensitivity was recorded either under passive viewing conditions (n = 9) or when the animals performed the attention task (n = 47), as outlined in the methods section of the main paper. Under passive viewing conditions monkeys fixated centrally while we presented bars of preferred orientation and 0.4° length for 500 ms centred on the neuron's RF. The luminance contrast (Michelson contrast) of the bars was 5%, 10%, 15%, 20%, 25%, 30%, 50%, and 100%. When contrast tuning was assessed while animals performed the attentionally demanding task, a bar of preferred orientation and a length of 0.4° was presented centered over the neurons RF (along with a corresponding bar in the opposite hemifield), while the luminance contrast of the bar was varied (5%, 10%, 15%, 20%, 25%, 30%, 50%, 100%). We determined contrast sensitivity by fitting a Naka-Rushton function to the mean firing rates that occurred during presentation of the different luminance contrasts (averaged over the entire response period from 50 ms after stimulus onset until 550 ms thereafter). The function took the form of:

$$R = offset + R_{\max} * \frac{c^n}{c^n + c50^n} \qquad \text{eq.1}$$

whereby R is the predicted response at contrast c. Offset corresponds to the spontaneous activity, R_{max} is the response at saturation level, c50 is the contrast at which half maximal response occurs and n determines the slope of the function. We used c50 as a measure of sensitivity for each cell. When contrast sensitivity was determined under attend-RF and attend-away conditions we used the attend-RF c50 for the analysis that is reported below. The effects of attention on contrast sensitivity per se are not the topic of the current paper, and they will be reported elsewhere. We recorded contrast sensitivity for a total of 28 cells at an eccentricity of 2-3°, the remaining 28 cells were recorded at an eccentricity of 6-7°. For these two samples we

did not find a significant difference in contrast sensitivity for the two eccentricities (p=0.600, rank sum test).
We subdivided each sample (the cells recorded at parafoveal and the peripheral sites respectively) into equal groups of 14 neurons, those with lower contrast sensitivity (large c50 values), and those with higher contrast sensitivity (small c50 values).
If contrast sensitivity determined whether attention increased or decreased the preferred length of a neuron we would expect to find that for both eccentricities the neurons with high contrast sensitivity would be influenced in the same manner, and the neurons with low contrast sensitivity would be influenced in the same manner, irrespective of whether neurons were recorded at parafoveal or peripheral locations. If, however, contrast sensitivity did not determine the effect of attention on length tuning we would expect the same effect of attention on neurons at parafoveal sites (irrespective of their contrast sensitivity) and a different effect for neurons from peripheral sites (also irrespective of their contrast sensitivity).
For the sample recorded at peripheral sites, we found that contrast sensitivity had no influence on length tuning. For both groups of neurons (those with high and those with low c50 values) we found an increase in preferred length when monkeys attended to the receptive field. This increase was significant for the sample with higher contrast sensitivity (p=0.004, signed rank test), while it was not significant for the sample with lower contrast sensitivity (p=0.173, signed rank test). Although the difference in the latter group was not significant, it showed the same basic pattern as the former group.

For the sample from parafoveal recording sites we have a corresponding finding. At this eccentricity attention reduced preferred length, and this reduction was not affected by the contrast sensitivity of the cells. When split into 2 groups of equal size, assigned according to their ranks of c50 values, we found that attention reduced the preferred length for the group with higher contrast sensitivity, and it also reduced the preferred length in the group with lower contrast sensitivity (see table 1 for details). Although the trend for reduced preferred length with attention to the receptive field was not significant in these subgroups (probably due to the small sample size) it mirrors our main basic finding, namely that attention reduces preferred length at parafoveal sites, and increases preferred length at more peripheral sites, irrespective of the contrast sensitivity of the neurons.

We did not find that splitting cells according to their contrast preference changed the sign of the effect of attention on length tuning. From this analysis we conclude that contrast sensitivity of neurons was not the factor which determined whether attention reduced or increased the preferred length of the neurons.

Comparison of preferred length for parafoveal and peripheral cells, grouped according to contrast sensitivity (c50)

Cell group		Median c50 (25, 75%ile)	Median preferred length attend RF (25, 75%ile)	Median preferred length attend away (25, 75%ile)	p-value (signed rank test)	Median Ratio of preferred length (25, 75%ile)
A	Parafoveal cells, low c50 (n = 14)	8.6 (7.5, 11.7)	0.365 (0.270, 0.635)	0.402 (0.240, 0.915)	0.104	0.914 (0.816, 1.056)
B	Parafoveal cells, high c50 (n = 14)	21.95 (15.7, 48.0)	0.440 (0.200, 1.510)	0.525 (0.260, 1.440)	0.241	0.910 (0.837, 1.049)
C	Peripheral cells, low c50 (n = 14)	9.425 (8.10, 10.1)	0.405 (0.240, 0.710)	0.290 (0.230, 0.510)	0.173	1.131 (1.077, 1.348)
D	Peripheral cells, high c50 (n = 14)	16.15 (14.70, 22.01)	0.900 (0.250,1.660)	0.477 (0.230, 1.405)	0.004	1.169 (0.963, 1.365)

Comparison of c50 values between parafoveal and peripheral cells

Parafoveal cells median (25, 75%tile) c50, n = 28	Peripheral cells median (25, 75%tile) c50, n = 28	p-value (rank sum test)
15.100	14.346	P = 0.600

(8.600, 21.950)		(9.425, 16.150)	

Comparison of c50 preference difference for the different groups (Kruskal Wallis ANOVA), Dunn's method				**Comparison of preferred length ratio (rank sum test)**
Cell group	Diff of Ranks	Q	P < 0.05	
B vs. C	30.036	4.872	Yes	
B vs. D	4.929	0.800	No	P = 0.041
D vs. A	25.107	4.073	Yes	
A vs. C	0.286	0.0463	No	P = 0.004

Supplementary Table 1: Contrast sensitivity and its relation to how attention affects length tuning. The top compartment of the table lists the c50 values for the different subgroups, along with the influence of attention on length tuning as a function of eccentricity. The middle compartment lists the contrast sensitivity for cells with parafoveal RFs vs. cells with more peripheral RFs. The lower compartment lists the statistics of pair-wise comparison of c50 values for the 4 different subgroups. The upper compartment shows that attending to the RF of a cell reduced the cell's preferred length for parafoveal RFs, and increased the preferred length for peripheral RFs, irrespective of the contrast sensitivity of the cells sample. The statistical analysis at the right of the lower table compartment demonstrates that the effect of attention on length tuning significantly differed for neurons that had peripheral RFs and neurons that had parafoveal RFs, irrespective of whether neurons preferred low or high contrast sensitivity. The test determined whether the ratio of preferred length under the attend RF and attend away condition differed significantly between group A (low c50, parafoveal) and group C (low c50, peripheral), and whether the same metric was significantly different between group B (high c50, parafoveal) and group D (high c50, peripheral). The difference was significant for both groups, although contrast sensitivity did not differ between the individual group comparisons.

Spatio-temporal frequency tuning:

In one monkey (monkey H) we measured the spatial frequency tuning of neurons at the parafoveal (n = 56 cells) and the more peripheral eccentricity (n = 47) prior to determining the effect of attention on length tuning. We found a significant difference in preferred spatial frequencies between the 2 samples ($p < 0.001$, t-test), whereby cells with parafoveal RFs preferred higher spatial frequencies than cells with more peripheral RFs (see table 2 for details). In principle the difference in preferred spatial frequency could account for the difference of the effect of attention on preferred length for the central and peripheral recording sites, rather than the difference in eccentricity per se, as SF and eccentricity co-vary. To test this we subdivided each cell sample into cells that preferred higher SFs and cells that preferred lower SFs. The cut-off for both groups was a preference of 3cyc/°, whereby cells with preference larger than 3 cyc/° were assigned to the high SF group, the remainder to the low SF group. This selection resulted in slightly unequal group sizes (see table 2), but it would otherwise have been impossible to determine which of the cells that preferred 3cyc/° (which comprised a large number from both groups) should be assigned to the high SF group. Following this division we determined whether the effect of attention on these subgroups was different, i.e. whether attention resulted in an increase in preferred length for cells that preferred low SFs and resulted in a decrease in preferred length in cells that preferred high SFs. We did not find any evidence that spatial frequency preference determined the effect of attention on length tuning. In both samples the effect of attention on length tuning persisted, even when cells were grouped according to preferred spatial frequency. In cells that were recorded at an eccentricity of ~ 2-3°, preferred length was reduced by attention irrespective of whether cells preferred high SF or whether they preferred low SFs. Conversely an increase of preferred length with attention was found in cells that were recorded at an eccentricity of ~7° irrespective of whether they preferred low or high SFs. Details and statistical analyses regarding these comparisons are provided in table 2.

Comparison of preferred length for parafoveal and peripheral cells, grouped according to spatial frequency (SF) preference

Cell group		Median (25, 75%ile) SF preference	Median (25, 75%ile) preferred length attend RF	Median (25, 75%ile) preferred length attend away	p-value (signed rank test)	Median Ratio of preferred length (25, 75%ile)
A	Parafoveal cells, low SFs (n = 29)	1.000 (1.000, 1.000)	0.290 (0.170, 1.200)	0.310 (0.180, 1.245)	0.094	0.989 (0.882, 1.120)
B	Parafoveal cells, high SFs (n = 27)	3.000 (3.000, 5.000)	0.440 (0.348, 0.556)	0.520 (0.414, 0.950)	0.005	0.859 (0.712, 0.980)
C	Peripheral cells, low SFs (n = 23)	3.000 (1.75, 3.000)	0.310 (0.180, 1.245)	0.235 (0.203, 0.745)	0.017	1.158 (1.032, 1.751)
D	Peripheral cells, high SFs (n = 24)	5.000 (5.000, 7.000)	0.375 (0.240, 1.340)	0.320 (0.230, 1.340)	0.074	1.017 (0.950, 1.078)

Comparison of SF preference between parafoveal and peripheral cells

Parafoveal cells mean (std) SF preference, n = 54	Peripheral cells mean (std) SF preference, n = 47	p-value t-test
3.906 (1.894)	2.622 (1.762)	P < 0.001

Comparison of SF preference difference for the different groups (Kruskal Wallis ANOVA), Dunn's method

Cell group	Diff of Ranks	Q	P < 0.05
B vs. C	67.134	7.902	Yes
B vs. D	21.375	2.604	No
D vs. A	22.360	2.850	Yes
A vs. C	23.399	2.872	Yes

Comparison of preferred length ratio (rank sum test)

P = 0.011

Supplementary Table 2: Spatial frequency (SF) tuning and its relation to how attention affects length tuning. The top compartment of the table lists the preferred SF values for the different subgroups, along with the influence of attention on length tuning as a function of eccentricity. The middle compartment lists the SF preference for cells with parafoveal RFs vs. cells with more peripheral RFs. The lower compartment lists the statistics of pair-wise comparison of SF preference for the 4 different subgroups. The upper compartment shows that attending to the cell's RF reduced the cell's preferred length for parafoveal RFs, and increased the preferred length for peripheral RFs, irrespective of the SF preference of the cells sample. The statistical analysis at the right of the lower table compartment demonstrates that the effect of attention on length tuning was not due to variation of spatial frequency preference. The test determined whether the ratio of preferred length under the attend RF and attend away condition differed significantly between group A (low SF, parafoveal) and group C (low SF, peripheral). For these two groups we did not find a significant difference in SF preference per se, but we still found that the effect of attention differed significantly depending on whether neurons had parafoveal or peripheral RFs.

Receptive field size:

We found a significant difference in receptive field size between the parafoveal and the peripheral recording sites ($p < 0.001$, rank sum test). However, the difference in RF size did not account for the differential effect of attention on length tuning at peripheral and at parafoveal sites. We subdivided each sample (parafoveally and peripherally recorded cells) into equally sized groups, with one group comprising of cells with larger receptive fields (larger than the

median of the respective sample) and those with smaller receptive field sizes. We then determined the effect of attention on preferred length for these groups. We found that for parafoveal recording sites attention significantly reduced the preferred length irrespective of the receptive field size of the cells (table 3). Conversely, for peripheral recording sites attention to the RF significantly increased the preferred length of the neuron, irrespective of the neuron's RF size (table 3). While there was no significant difference between receptive field sizes of the parafoveal group with large receptive field sizes, and the peripheral group with small receptive field sizes, we nevertheless found a significant decrease of preferred length under the attend-RF condition in the former group and a significant increase in preferred length under the attend-RF condition in the latter group (table 3 for details). From this we conclude that receptive field size does not determine whether attention reduced or increases the preferred length of V1 neurons.

Comparison of preferred length for parafoveal and peripheral cells, grouped according to receptive field size

Cell group		Median (25, 75%ile) RF size	Median (25, 75%ile) preferred length attend RF	Median (25, 75%ile) preferred length attend away	p-value (signed rank test)	Median Ratio of preferred length (25, 75%ile)
A	Parafoveal cells, small RFs (n = 30)	0.275 (0.182, 0.315)	0.448 (0.320, 0.760)	0.522 (0.340, 0.920)	0.003	0.918 (0.863, 1.000)
B	Parafoveal cells, large RFs (n = 30)	0.519 (0.464, 1.194)	0.420 (0.270, 0.780)	0.465 (0.315, 1.020)	0.043	0.898 (0.750, 1.049)
C	Peripheral cells, small RFs (n = 27)	0.576 (0.517, 0.625)	0.280 (0.203, 0.883)	0.270 (0.194, 0.518)	0.046	1.106 (1.017,1.847)
D	Peripheral cells, large RFs (n = 28)	1.265 (0.855, 2.138)	0.385 (0.242, 1.277)	0.253 (0.195, 1.203)	0.010	1.077 (1.000, 1.298)

Comparison of RF size between parafoveal and peripheral cells

Parafoveal cells median (25, 75%ile) RF size, n = 60	Peripheral cells median (25, 75%ile) RF size, n = 55	p-value Rank sum test
0.351 (0.275, 0.519)	0.717 (0.576, 1.326)	P < 0.001

Comparison of RF size difference for the different groups (Kruskal Wallis ANOVA)

Cell group	Diff of Ranks	Q	P < 0.05
D vs. A	80.071	9.139	Yes
D vs. B	32.171	3.672	Yes
B vs. C	4.206	0.475	No
C vs. A	43.694	4.940	Yes

Comparison of preferred length ratio (rank sum test)

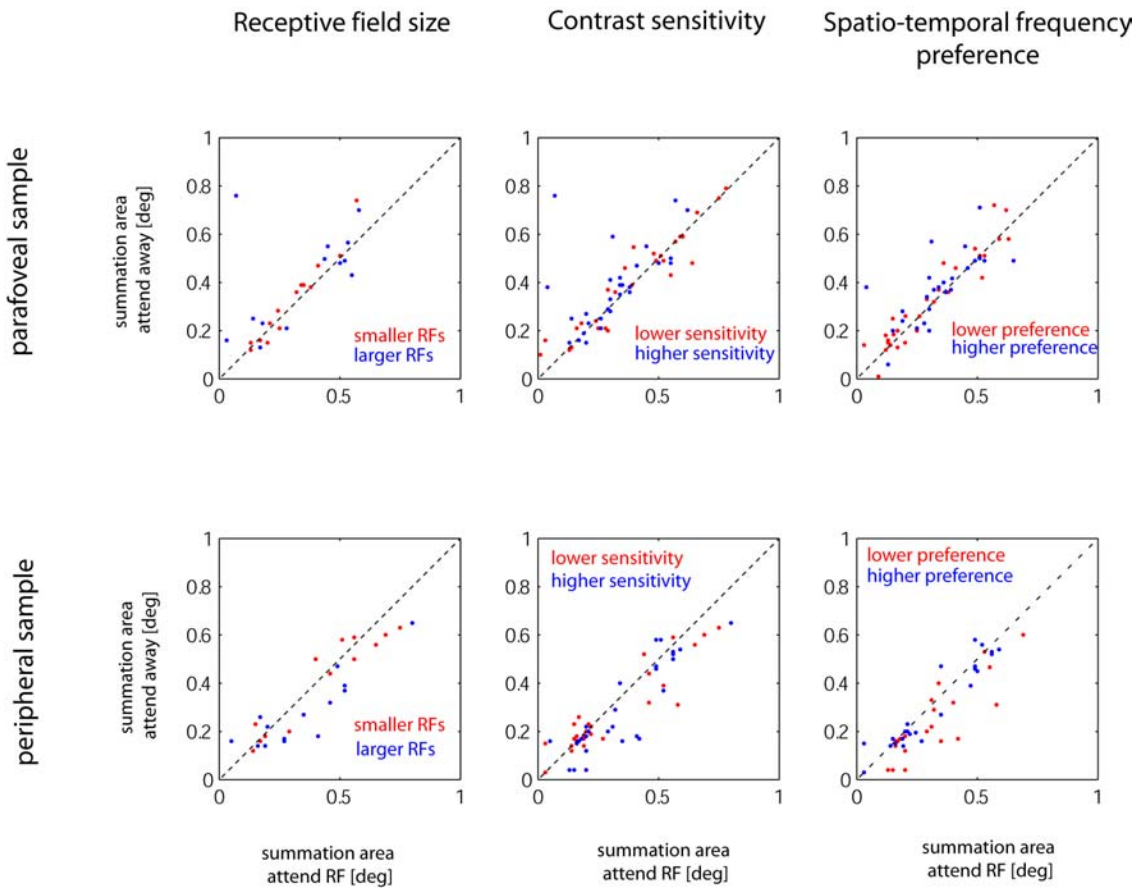
P < 0.001

Supplementary Table 3: Receptive field (RF) size and its relation to how attention affects length tuning. The top compartment of the table lists the RF size values for the different subgroups, along with the influence of attention on length tuning as a function of eccentricity. The middle compartment lists the RF size for cells with parafoveal RFs vs. cells with more peripheral RFs. The lower compartment lists the statistics of pair-wise comparison of RF size for the 4 different subgroups. The upper compartment shows that attending to the RF of a cell reduced the cell's preferred length for parafoveal RFs, and increased the preferred length for

peripheral RFs, irrespective of the RF size of the cells sample. The statistical analysis at the right of the lower table compartment demonstrates that the effect of attention on length tuning was not due to variation of receptive field size. The test determined whether the ratio of preferred length under the attend-RF and attend-away condition differed significantly between group B (large RFs, parafoveal) and group C (small RFs, peripheral). For these two groups we did not find a significant difference in RF size per se, but we still found that the effect of attention differed significantly depending on whether neurons had parafoveal or peripheral RFs.

The above data demonstrate that neither receptive field size, nor contrast sensitivity, nor spatial frequency preference per se determine the effect of attention on spatial integration. It could still be the case that ceiling effects, or some other non-uniformity in the data, contribute to our finding of changed summation area (or other parameters of the DOG model). Supplementary Figure 1 provides evidence that this is not the case. It plots the summation area for the subgroups of cells when animals attended to the receptive field of the neuron under study and when they attended away. It shows that e.g. cells with relatively lower spatial frequency preference are equally likely to show changes in summation area as are cells from the group that prefers higher spatial frequencies, and in neither of the two groups are the effects limited to cells with overall smaller or larger summation areas.

Supplementary figure 1:



Supplementary Figure 1: Attention induced changes in the size of the summation area for different subgroups of cells. The left column shows cells from the parafoveal sample (top) and from the peripheral sample (bottom), that were split according to their respective receptive field size (each sub-sample was split relative to the median receptive field size for of that sample). Red dots show summation areas for cells with relatively smaller receptive fields, blue dots summation areas of cells with relatively larger receptive fields. The middle column shows the respective data when cells are ordered according to contrast sensitivity (C50). The right column shows the summation area as a function of attention when cells are separated according to spatial frequency preference.

Supplementary information 2: Model comparisons

As described in the main paper, we attempted to fit our data with a variety of different models/sub-models. These fitting procedures revealed that a DOG model consistently yielded significantly better fits than a ROG model. Moreover, it revealed that constraining the summation area such that it had to take the same value in the attend-away and attend-RF condition resulted in the largest deterioration of fit quality. From this we deduce that our data are best explained by a model that allows the spatial summation area to vary depending on whether attention was directed to or away from the RF of the neuron under study. Previous investigations in the anesthetised animal have argued whether the increase in length/size tuning at low contrast is best described by a DOG or a ROG model, and whether these changes can be accounted for by changes in summation area in conjunction with gain changes, or whether changes in gain alone are sufficient to explain the data [1, 2]. At first glance our results seem to bear on these analyses, however, there are important distinctions that need to be kept in mind. The studies by Sceniak [2] and Cavanaugh [1] investigated mechanisms of spatial integration as a function of contrast in V1. Thus, a change in spatial integration under those circumstances might possibly be explained by differences in contrast sensitivity between excitatory network and inhibitory networks, while in our study feedback from attentional control centres (by way of other visual and non-visual areas), possibly in conjunction with different neuromodulator levels, would determine spatial integration properties. Due to these differences, we do not think our data can be used to argue which model is more suited to describe changes in spatial integration under the circumstances employed by Cavanaugh et al. [1] or Sceniak et al. [2].

Supplementary information 3: Identification of DOG model parameters

As discussed in the main paper it could be argued that the direct thalamic input should be identified largely with the summation gain, while the summation area would relate to excitatory intra-cortical lateral connections. Within this framework the inhibitory gain would be identified with: (1) feed-forward connections terminating on inhibitory basket cells (thereby providing the inhibitory gain control within the CRF), (2) lateral and feedback connections terminating on local inhibitory neurons, or (3) intra-cortical long range connections terminating on inhibitory interneurons. Lateral and feedback terminals on inhibitory interneurons would then be responsible for the size of the inhibitory area. The argument that the summation gain should largely be identified with feed-forward thalamocortical neurons (in conjunction with recurrent local excitatory connections) is based on the average size of the summation area of ~0.5° in our data set, which is well within the limits of the pooling that has been described for low contrast stimuli [3, 4].

Although there is evidence to support these ideas, some of them face explanatory difficulties when looked at in detail, and we will describe some of the caveats in the following paragraph.

It has been suggested that suppressive surround modulation is mostly due to feedback from other areas [1, 4, 5], and these should thus be identified with the inhibition gain and inhibition area of the DOG model. The problem with this proposal is that the feedback would need to target inhibitory interneurons (feedback connections are mostly glutamatergic [6]), but feedback has been shown to mostly target pyramidal cells, while terminals on inhibitory interneurons are rare [6-8]. Thus, despite support from electrophysiological studies [1, 4, 9, 10], identification of feedback with the inhibitory parameters of the DOG model is currently not straightforward. An account whereby lateral connections contribute to the inhibitory parameters of the DOG model does not encounter these explanatory difficulties in terms of the underlying anatomical substrate, as lateral connections within primary visual cortex target inhibitory as well as excitatory neurons [11], and inhibitory long range connections have been described [12]. However, the speed of

surround suppression has been used as an argument against the contribution of lateral connections [9] to inhibition from outside the CRF.

To identify the inhibition gain exclusively with modulatory *surround* mechanisms would additionally be misleading, as inhibition acts locally (i.e. within the CRF) through specific cell types, likely mediating gain control [13], while other types have been suggested to serve specific gating functions and pathway switching [13].

The identification of feedback with mostly inhibitory surround modulation has additional problems. It discounts that attention mediated firing rate enhancement in visual cortical areas is likely to be mediated by feedback from higher areas [14, 15]. These feedback connections must therefore include the CRF and so cannot be confined to the surround. In short, feedback cannot be exclusively identified with inhibitory mechanisms, unless one proposes that an increase in inhibitory drive results in increased synchrony among neurons, by which firing rates can be increased [16-18]. In principle excitatory feedback could be confined to the CRF/summation area while inhibitory feedback (via local inhibitory neurons) cover the CRF and surround. However, this would require highly specific wiring pattern, as it would have to be the case for each individual neuron. Whether this specificity exists is currently unknown.

These arguments demonstrate that an identification of the different parameters of the DOG model is difficult once a certain level of detail is taken into account (and a much greater level of detail could be discussed). We thus propose to use the outlined form of the model as a preliminary approximation, well aware that further studies are required to reveal the contributions of different network components to spatial integration and to attentional influences in striate and extrastriate cortical areas.

Supplementary information 4: Time course of attentional modulation

Previous studies have repeatedly reported that the time course of attentional modulation is delayed relative to response onset (e.g. [19]), which is similar to our previous finding of the application of Acetylcholine in V1 [20]. In our current study we also find that attentional modulation is most prominent during later parts of the response (see figure 4 of the main paper). However, it should be noted that attentional modulation in area V4 has been shown to vary with task timing [21], and can occur early during responses in V1 under appropriate task settings [22]. The absence of attentional modulation during the early part of the response in our study may thus be partially due to the fact that the behaviorally relevant change was delayed relative to stimulus onset, rather than being a fixed feature of neuronal responses.

Supplementary information 5: 1-D versus 2-D measurements

The quantitative measurements in our study were performed with bars of varying length, but fixed width. Thus the measurements in our study are basically 1-dimensional. Other studies investigating the effect of varying size on spatial integration have often used 2-dimensional stimuli [1, 2, 4] (but see [3]). To investigate whether the effects of attention transfer from 1-D to 2-D stimuli we recorded an additional 27 cells in monkey H, where we presented concentric gratings of 8 different diameters (0.2, 0.4, 0.6, 0.8, 1.2, 1.6, 2.4, and 3.2°) centered on the neuron's RF, and determined spatial integration when the monkey attended to the neuron's RF compared to when he attended away. These recordings were performed at parafoveal recording sites. For this sample we found the same basic results as we had previously found for the 1-D stimuli, namely that attending to the neuron's RF resulted in a significant decrease of the preferred size (median preferred size attend RF: 0.420 [0.150, 0.487], median preferred size attend away: 0.460 [0.393, 0.548], p=0.004, signed rank test), and a significant decrease in the summation area (median attend RF: 0.386 [0.113, 0.484], median attend away: 0.479 [0.376, 0.583], p=0.016, signed rank test, numbers in square brackets represent 25 and 75 percentiles) while the other parameters of the DOG model were not significantly affected by attention. This control demonstrates that the result of our main study is not a result of a choice of 1-D stimuli.

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