

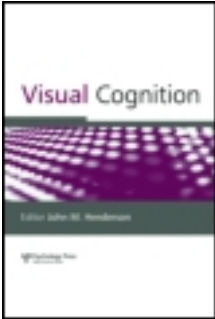
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Attentional attraction of receptive fields can explain spatial and temporal effects of attention

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A multitude of attentional effects were found at both the neural and behavioural levels of perception; however, the nature of the attentional mechanism is an unsettled issue. It is typically assumed that the fundamental impact of attention is enhancement of neuronal responses, but some attentional effects are difficult to explain by such gain modulations. Here we offer a different view: We suggest that the most fundamental impact of attention is the attraction (shift) of receptive fields towards the attended location. We further show, both conceptually and by model simulations, that this attraction of receptive fields can explain a diverse range of attentional effects, spatial as well as temporal, linking physiological measurements at the unit level with psychophysical observations (e.g., enhanced contrast sensitivity, enhanced spatial resolution, the Mexican-hat profile of attention, prolonged perceived duration, prior entry, degraded temporal resolution).

Keywords: Visual attention; Shift of receptive fields; Spatial effects of attention; Temporal effects of attention; Computational model.

The term “spatial attention” refers to processes that select a location in space and grant priority to information gathered at that location. Attentional effects were found for both neuronal responses (e.g., Mountcastle, Motter, Steinmetz, & Sestokas, 1987; Reynolds, Chelazzi & Desimone, 1999; Treue & Maunsell, 1999; Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006) and behavioural responses (e.g., Carrasco, Ling, & Read, 2004; Rolke, Dinkelbach, Hein, & Ulrich, 2008; Visser & Enns, 2001; Yeshurun, 2004). Most of these effects

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concern spatial aspects such as enhanced spatial resolution (e.g., Yeshurun & Carrasco, 1998, 2008), enhanced contrast sensitivity (e.g., Pestilli & Carrasco, 2005), enhanced neuronal responses at the focus of attention (e.g., McAdams & Maunsell, 1999; Reynolds, Pasternak, & Desimone, 2000), and suppressed neuronal and behavioural responses at the surrounding of the attentional focus (e.g., Cutzu & Tsotsos, 2003; Vanduffel, Roger, Tootell, & Orban, 2000). Some effects of spatial attention were also found in the temporal domain, including degraded temporal resolution (e.g., Hein, Rolke & Ulrich, 2006; Yeshurun & Levy, 2003), prior entry (e.g., Shore, Spence, & Klein, 2001), and prolonged perceived duration (e.g., Enns, Brehaut, & Shore, 1999; Yeshurun & Marom, 2008).

Many models attempted to explain the mechanism by which attention modulates visual perception (e.g., Anderson & Van Essen, 1987; Desimone & Duncan, 1995; Ghose & Maunsell, 2008; McAdams & Maunsell, 1999; Olshausen, Anderson, & Van Essen, 1993; Pestilli, Ling, & Carrasco, 2009; Reynolds et al., 1999; Treue & Martinez-Trujillo, 1999; Tsotsos et al., 1995; Womelsdorf, Anton-Erxleben, & Treue, 2008; see Reynolds & Heeger, 2009, for a review). These models were able to explain some attentional effects but not others. Typically, it was assumed that the main impact of attention is a gain modulation: Attention enhances the neuronal responses at the attended location (e.g., McAdams & Maunsell, 1999; Treue & Martinez-Trujillo, 1999). The recently suggested “Normalization model of attention” (Reynolds & Heeger, 2009) showed how a combination of an attentional gain and a suppressive surround, both with a dynamic “diameter”, can explain a diversity of observed attentional phenomena. Still, some effects of attention remain unexplained by this model. Specifically, this model cannot explain the neurophysiological finding that attention shifts the centres of receptive fields (RFs) towards the attended location (e.g., Connor, Gallant, Preddie, & Van Essen, 1996; Connor, Preddie, Gallant, & Van Essen, 1997; Quraishi, Heider, & Siegel, 2007; Womelsdorf et al., 2006, 2008). Several models attempted to explain how the observed RF changes were a consequence of gain modulations (Compte & Wang, 2006; Womelsdorf et al., 2008). However, the results of these models do not coincide with some aspects of the observed phenomena (see analysis in Miconi & VanRullen, 2011). Miconi and VanRullen (2011) suggested a feedback model that extends the results of the normalization model (Reynolds & Heeger, 2009) explaining changes in size and position of RFs based on short range inhibition and feedback excitation via reciprocal connections. Similarly to previous studies, however, Miconi and VanRullen do not refer to attentional effects in the temporal dimension of perception.

We present here a simple feed-forward mechanism that can explain a multitude of attentional effects. We propose that not gain, but the attraction (shift) of RFs towards the focus of attention is the primary impact of attention. We show that it is straightforward and simple to explain enhanced gain and many

additional attentional modulations, spatial as well as temporal, by such an Attentional Attraction Field (AAF). To our knowledge, no single model can account for all the phenomena that the AAF can account for. To test the idea of the attentional attraction field, we implemented a feed-forward model. For each of the attentional effects described later, we shall first give an intuitive account followed by the results of the model simulations.

THE ATTENTIONAL ATTRACTION FIELD MODEL

The core idea of the Attentional Attraction Field (AAF) model is the conception of attention as an attraction field. By this conception attention attracts the centres of RFs towards the focus of attention such that RFs that are closer to the centre of attention are affected more by this attraction than RFs that are farther away. It is further assumed that the power of the attraction field is proportional to the concentration of attention: When attention is spread there is no attentional modulation, whereas a narrowly focused attention leads to a large modulation of RFs.

The model consists of an input layer, representing the stimulus field and two layers of neurons. Neurons in the first layer (L1) receive input from overlapping rectangular RFs in the stimulus field. The location of these RFs might change as a result of attention as explained below. Neurons in the second layer (L2) receive direct input from a fixed set of neurons in overlapping rectangular areas of L1.

A receptive field of an L2 neuron is defined as the union of the RFs of its L1 afferent (input providing) neurons. Thus, the structure of the model reflects a hierarchy of layers in which information from the lower layers is converged while transferred up the hierarchy. As in the visual hierarchy, an L2 neuron receives information from a larger portion of the stimulus field than an L1 neuron.

A neuron's response was implemented as the weighted sum of its input, followed by thresholding. Thus, the activation of an L1 neuron is determined by the luminance in its RF, and the activation of an L2 neuron is determined by the activation of its afferent neurons.

Attention was modelled as a Gaussian attraction field $G(r, \sigma)$ that is centred at a specific location in the stimulus field. The parameter r represents the distance of an RF's centre from the centre of attention, and the parameter σ represents the spread of attention. A small σ implies narrow (focused) attention and a large σ implies diffused attention. Importantly, the only attentional effect that was explicitly implemented in the model was the shift of RFs of first layer neurons towards the focus of attention. All other effects, described later, are indirect consequences of this shift (a mathematical formulation of the model is included in the Appendix).

Induced changes in location and size of receptive fields

We shall first show how the shift of RFs towards the focus of attention at some layer of the visual hierarchy propagates up to subsequent layers and induces a change in position and shape of RFs of higher layers' neurons.

Let us assume that attention shifts the RFs of neurons at some layer L towards the focus of attention, and let N be a neuron at a subsequent layer of the visual hierarchy receiving input from neurons in layer L . The RF of N is defined as the unified area of the RFs of its afferent layer L neurons. Suppose attention is focused within the RF of N : As a result of the shift of RFs of the afferent layer L neurons towards the focus of attention, the unified area of the afferent RFs is reduced and thus the extent of the RF of N is reduced accordingly (Figure 1A). In other words the RF of N shrinks. An attentional shrinkage of RFs was reported by several studies (e.g., Connor et al., 1997; Moran & Desimone, 1985; Womelsdorf et al., 2006). Yet when attention is directed to a location outside of the RF of N , RFs of the afferent neurons that are closer to the attended location are attracted more than RFs that are farther away. Thus, the unified area of these

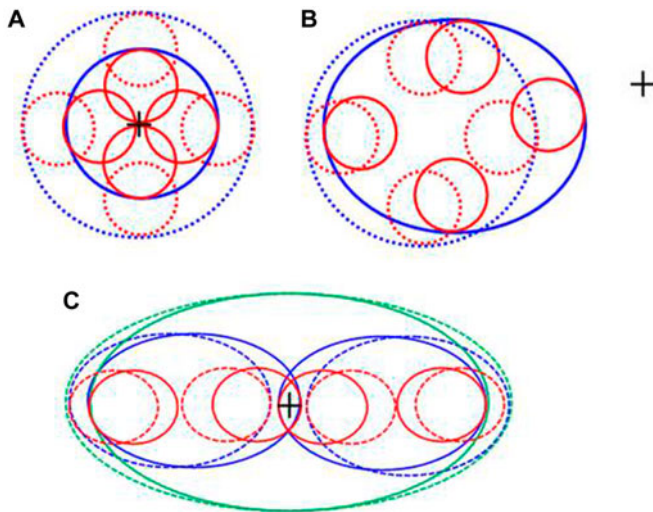


Figure 1. The influence of attention on RFs: (A) When attention is directed to a location (black cross) within the RF (dotted blue) of a higher layer neuron, N , the shift of RFs of lower layer afferent neurons (red circles) towards the focus of attention results in the shrinkage of the RF of N (solid blue). (B) When attention is directed to a location outside the RF of N (black cross) the nonlinear attraction of the RFs towards this location results in the elongation of the RF of N and its shift towards the focus of attention. (C) RFs of 3 consecutive layers in the visual hierarchy. The attentional attraction shifts the RFs of the lowest layer, L (red circles) towards the focus of attention. This shift propagates up the visual hierarchy and leads to a shift and an elongation of the RFs of the subsequent layer, $L+1$ (blue) and a shrinkage of the $L+2$ RF (green).

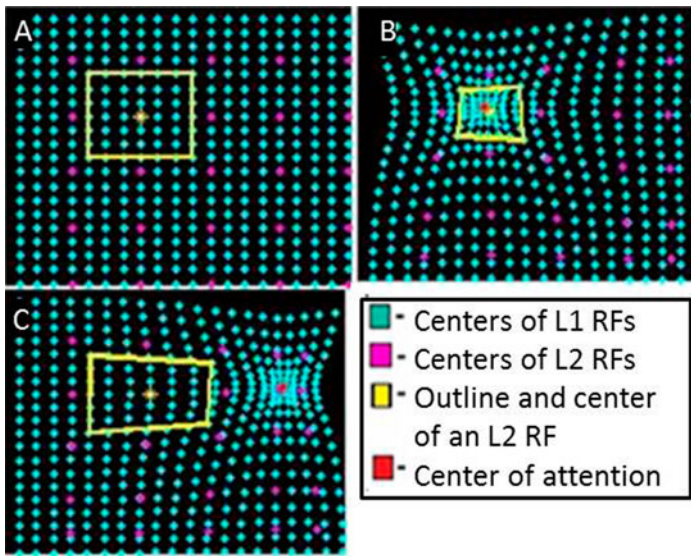


Figure 2. The simulated attentional modulation of RFs: Cyan and magenta symbols denote RF centres of neurons of the first layer (L1) and the second layer (L2), respectively. The yellow asterisk and rectangle mark the centre and boundaries respectively of the RF of a specific L2 neuron. The centre of attention is marked by a red asterisk. (A) RF centres of L1 neurons and the outline of an L2 RF without attention. (B) When attention is focused inside the RF of the L2 neuron, the attraction of L1 RFs towards the centre of attention shrinks the RF. (C) When attention is focused outside the RF of the L2 neuron the attraction of L1 RFs elongates the RF of the L2 neuron and shifts its centre towards the focus of attention. The attentional attraction leads also to a distortion of the shape of the RF.

RFs increases and its centre of gravity moves towards the attended location. In other words, the RF of the higher layer neuron, N , is expanded and shifted towards the attended location (Figure 1B). Such an attentional expansion of RFs was also reported more recently (Anton-Erxleben, Valeska & Treue, 2009). Figure 1C demonstrates how these effects further propagate up the visual hierarchy.

Figure 2 displays the results of the model simulation: as expected the shift of RFs of the lower layer neurons towards the focus of attention results in either a shrinkage (Figure 2B) or elongation (Figure 2C) of the RF of the higher layer neuron, depending on the locus of the attentional focus.

SPATIAL ASPECTS OF THE ATTENTIONAL ATTRACTION FIELD

Enhanced response

According to the AAF model, focusing attention on a specific location attracts the centres of RFs towards the attended location. Thus, when attention is directed towards a stimulus, the shift of RFs towards that location increases the overlap

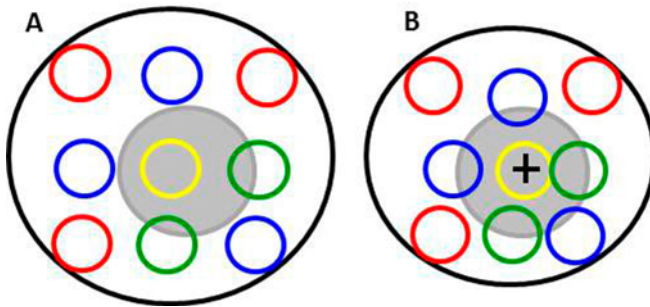


Figure 3. The effect of attention on the spatial relationship between RFs and the attended stimulus. (A) RFs of lower layer (L1) neurons (coloured circles) and the RF of the corresponding higher layer (L2) neuron (black circle) overlaid on a visual field containing a single stimulus (grey filled circle) without attention. (B) When the focus of attention is on the stimulus (black cross), the attraction of L1 RFs increases the overlap of some of the RFs with the stimulus (green circles). This should lead to a higher activation of the corresponding neurons. The attraction also brings the stimulus into some RFs that resided outside the area of the stimulus without attention (blue circles); thus, the number of neurons responding to the stimulus increases. Some neurons will not be affected by the attentional modulation either because their RF was completely embedded within the area of the stimulus even without attention (yellow circle) or because it remained outside the stimulated area even with attention (red circles). The excitation of the corresponding higher layer neuron will increase as the result of the higher excitation of its afferents.

between adjacent RFs and the stimulus. This results in an enhanced response of the corresponding neurons, as a larger portion of the stimulus falls within their RF. The shift may also “bring” the stimulus into RFs that did not overlap the stimulus at all without attention, increasing the overall number of neurons that respond to the stimulus (Figure 3). Thus, the AAF model involves attentional modulations at the single unit level as well as at the population level. The enhanced response at the modulated layer propagates to all neurons up the visual hierarchy that receive direct or indirect input from this layer. To test whether the attraction of RFs, which is the sole direct modulation exerted by the AAF model, can indeed lead to enhanced response at the focus of attention, we simulated the activity of neurons in the first layer (the only layer on which attention is operating directly) in response to a small square stimulus. Figure 4 presents the outcome of this simulation. The top panels of the figure demonstrate the overlap between L1 RFs and the stimulus with and without attention. The brightness level at each position in the bottom panels represents the activity level of the corresponding neuron. As a consequence of the attentional attraction of RFs towards the square’s centre, there is, as expected, both an increase in the number of neurons that respond to the square, and an enhanced activity of individual neurons.

Enhanced neuronal responses when attention is directed to a stimulus inside the neuron’s RF were found by numerous neurophysiological studies (e.g., McAdams & Maunsell, 1999; Mountcastle et al., 1987; Spitzer, Desimone &

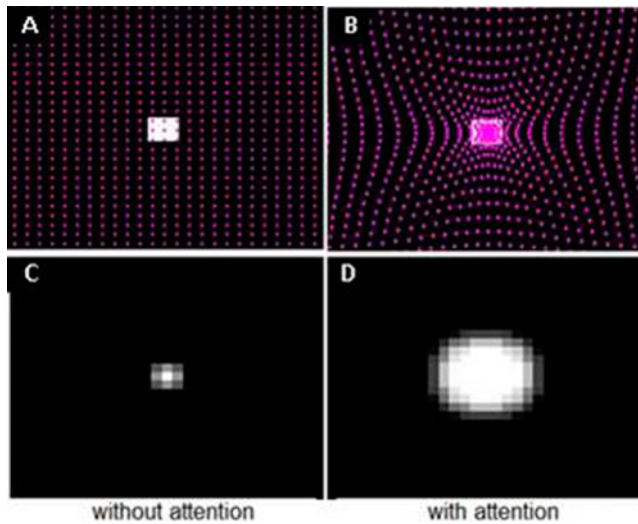


Figure 4. Simulated activity of neurons in the first layer in response to a square stimulus. The top images present the stimulus overlaid with the centres of RFs: (A) without attention, (B) with attention focused on the centre of the square. The bottom images show the corresponding neuronal response to the square. The brightness level at each position represents the activity level of the corresponding neuron. (C) Simulated activity without attention. (D) Simulated activity with attention. The attentional attraction of RFs increases the overlap between adjacent RFs and the stimulus, resulting in a larger neuronal population that responds to the stimulus and an increased activity of individual neurons at the attended location. To view this figure in colour, please see the online issue of the Journal.

Moran, 1988; Treue & Maunsell, 1996, 1999; Williford & Maunsell, 2006). The fact that a shift of RFs can lead to gain enhancement, both at the layer that is directly affected by the shift modulation and at subsequent layers in the hierarchy, implies that such a shift could underlie behavioural phenomena that may be induced by enhanced gain such as increased contrast sensitivity (e.g., Carrasco, Penpeci-Talgar, & Eckstein, 2000; Pestilli & Carrasco, 2005) and higher apparent contrast at the attended location (e.g., Carrasco et al., 2004).

Noteworthy, the model predicts that the magnitude of the attentional enhancement for a given neuron depends on the degree to which the attentional attraction increases the overlap between the stimulus and the RF of that neuron: The larger the increase in the portion of the RF that overlaps the stimulus, the larger the enhancement of neuronal response (green and blue circles in Figure 3). Conversely, when the attentional attraction does not change the overlap percentage between the neuron's RF and the stimulus, for example when the stimulus remains outside the RF even with the attentional attraction (red circles in Figure 3), or when there is full overlap with and without attention (yellow circle in Figure 3), the corresponding neuron's response will not be affected by attention. Furthermore, in some cases, (e.g., when the stimulus has an irregular

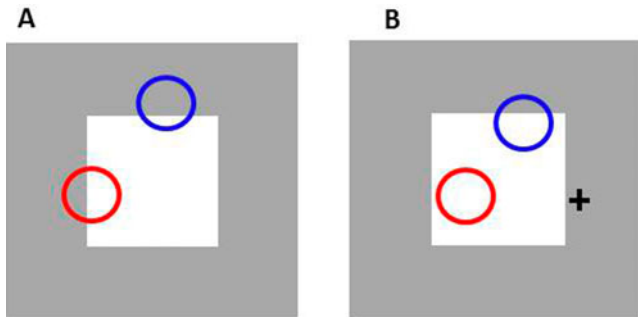


Figure 5. Attentional shift of RFs may lead to a reduction in the portion of the RF that overlaps the stimulus and hence to a decrease in the corresponding neuron's response. (A) A rectangular grey stimulus with a hole in its centre, and RFs of two L1 neurons, without attention. (B) When attention is directed to the location marked by the cross, the shift of RFs towards the focus of attention leads to a decrease in the overlap between these RFs and the stimulus. To view this figure in colour, please see the online issue of the Journal.

shape, or when the luminance of the stimulus is not uniform), the attraction of RFs to an attended location might shift an RF to a location that evokes a smaller neuronal response with than without attention. For example, the shift might decrease, or even eliminate the overlap between an RF and the stimulus (Figure 5).

Another factor that influences the magnitude of the attentional enhancement of a neuron's response is the placement of the stimulus within its RF: Attending a stimulus that is placed near the borders of the RF results in a smaller increase in the activation of the corresponding neuron, N , than when the attended stimulus is placed at the centre of the RF. This is because, in the former case, some of the neurons from preceding layers that are affected by the attraction of their RFs to the attended stimulus are not afferents of the neuron N , and therefore do not influence its activation. Indeed, results of experiments with a single stimulus in a neuron's receptive field demonstrate large response variability (see summary in Luck, Chelazzi, Hillyard, & Desimone, 1997).

The Mexican hat profile of attentional modulation

As described previously, the attentional attraction field causes a shift of RFs towards the focus of attention. This shift results in an increased density of RFs at regions adjacent to the focus of attention, but due to its nonlinearity it also leads to a decreased density of RFs at the attentional surrounds (Figure 6). The outcome is a Mexican hat density function of RFs. The exact shape of this function is determined by the strength of the attentional modulation, which in the model is defined by the diameter of the attended area—a narrower focus of attention leads to a stronger attentional attraction and a steeper density function.

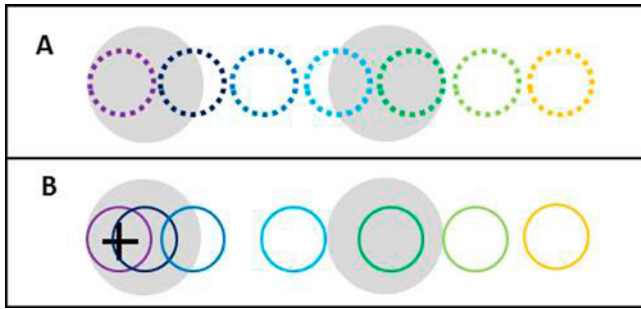


Figure 6. The position of RFs (coloured circles) with respect to two stimuli (grey filled circles): (A) Without attention. (B) With attention directed to the location marked by the black cross: The distribution of the RFs without attention was modelled as uniform. The AAF model predicts a nonlinear shift of RFs towards the focus of attention leading to an increased density of RFs at the attended location and a decreased density at its surrounds. To view this figure in colour, please see the online issue of the Journal.

Figure 7 displays Mexican hat shaped density functions of RFs, resulting from various diameters of the attended area, as simulated by the model. This prediction, namely the Mexican hat modulation of the density of RFs around the focus of attention, is yet to be tested.

A straightforward result of the Mexican Hat shaped RFs' density function is that the response enhancement at the centre of attention should be accompanied by response suppression at the surrounds of attention. To demonstrate this prediction, we simulated the response of two neurons (N_1 , N_2) from the second

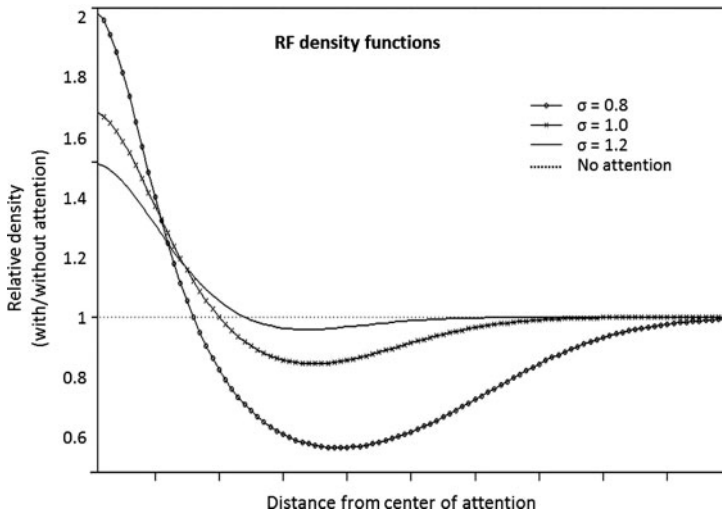


Figure 7. RFs' relative density functions: The density of RFs with attention with respect to the density of RFs without attention, as a function of the distance from the centre of attention and the diameter of the attended area (σ). This function has the shape of a Mexican hat. See Appendix for additional details.

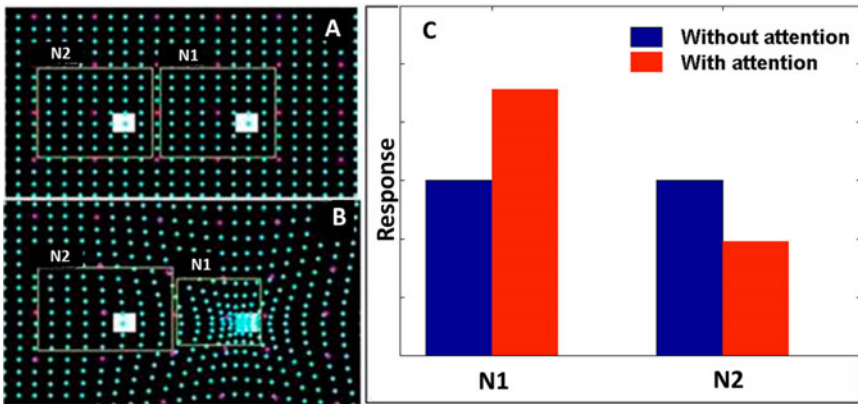


Figure 8. Two white square stimuli overlaid by the centres of RFs from the first (cyan) and second (magenta) layers. The yellow rectangles mark the outlines of RFs of two second layer neurons (N1, N2). (A) RFs' layout without attention. (B) RFs' layout when attention is focused on the stimulus in N1's RF. (C) Simulation results showing the response of N1 and N2 to the stimuli in their RFs without and with attention. The attraction of RFs towards the centre of attention reduces the density of RFs at the surrounds of the attentional focus, resulting in response suppression surrounding the region of enhanced activity. To view this figure in colour, please see the online issue of the Journal.

layer of our model to stimuli in their RFs when attention is focused on the stimulus in N1's RF, and the stimulus in N2's RF falls in the suppressive surround of attention. As can be seen in Figure 8, in comparison to their response without attention, the response of N1 is enhanced while the response of N2 is suppressed.

Although the classical views of spatial attention as a spotlight (e.g., Posner, 1980; Posner, Snyder, & Davidson, 1980), zoom lens (e.g., Eriksen & Hoffman, 1972; Eriksen & St. James, 1986), or gradient (e.g., LaBerge, 1983; LaBerge & Brown, 1986) referred only to the perceptual facilitation exerted by attention, recent evidence in support of a suppressive annulus surrounding the area of attentional enhancement was reported at both neuronal and behavioural levels (e.g., Cutzu & Tsotsos, 2003; Hopf et al., 2006; Müller & Kleinschmidt, 2004; Sundberg, Mitchell, & Reynolds, 2009). Moreover, some studies hypothesized that the attentional modulation, namely the attentional enhancement and suppressive surround, has a Mexican hat profile and presented evidence in support of this hypothesis (e.g., Caparos & Linnell, 2009; Heinemann, Kleinschmidt, & Müller, 2009; Hopf et al., 2006; Müller, Mollenhauer, Rosler, & Kleinschmidt, 2005). For example, Caparos and Linnell (2009) examined attentional modulation under different perceptual loads. They found that, whereas under low perceptual load attention had a gradient profile, it followed a Mexican hat profile when perceptual load was high. It is likely that under conditions that do not entail narrowly focused attention, it is more difficult to measure the suppressive surround.

Most models of attention dealt with the enhancement effect of the attentional modulation (e.g., McAdams & Maunsell, 1999; Mountcastle et al., 1987; Reynolds & Heeger, 2009), others dealt with the suppressive surround (e.g., Tsotsos et al., 1995), but to our knowledge there is no model that explicitly accounts for both phenomena. Conversely, as shown in Figure 7, the Mexican hat profile is a natural result of the attraction of RFs towards the focus of attention. Hence, the AAF model offers a parsimonious account as it proposes that the enhancement of neuronal response to attended stimuli and suppression of neuronal response to stimuli at the surround of attention, phenomena that are usually attributed to different mechanisms, may be due to a single mechanism.

Biased competition

Some studies have found a “Biased Competition” phenomenon: When both preferred and nonpreferred stimuli are placed within a neuron’s RF, the allocation of attention to either stimulus “biases” the neuron’s response towards the response to that stimulus when presented alone. Specifically, when the preferred stimulus was attended a sizeable neuronal response was observed, as expected given that the preferred stimulus is presented within the neuron’s RF. However when the nonpreferred stimulus was attended, a significant decrease in the neuron’s response was observed. When attention was directed away from both stimuli the responses to the pair typically fell between the responses evoked by the individual stimuli. (e.g., Desimone & Duncan, 1995; Moran & Desimone, 1985; Reynolds et al., 1999; Treue & Maunsell, 1996). The AAF model can account for this result. Suppose a neuron, *N*, receives its input from a set of afferents with some preference. When both, a preferred stimulus and a nonpreferred one are placed in the neuron’s RF, its response is expected to be in between the responses evoked by the individual stimuli. Attending any of the stimuli leads to a concentration of the RFs of the afferent neurons on the attended stimulus (Figure 9a and b); thus, the majority of the input of *N* is driven by the response to the attended stimulus and therefore the response of *N* is expected to be biased towards its response to that stimulus when placed alone in its RF.

We simulated the setting practiced in the reported experiments and evaluated the response of an orientation sensitive second layer neuron, when two bars were placed in its RF—one bar with the neuron’s preferred orientation (vertical) and the other with a nonpreferred orientation (horizontal). Orientation selectivity was implemented by using first layer (L1) vertically elongated rectangular RFs. (see the Simulation parameters section in the Appendix for details). Neurons with such RFs prefer stimuli whose orientation is similar to their elongation axis: When the size of the narrow dimension of an elongated stimulus is of the same order of magnitude as (or smaller than) the RF’s vertical dimension, there will typically be a larger degree of overlap between the stimulus and the RF when the orientation of the stimulus is the same as that of the RF than when it is

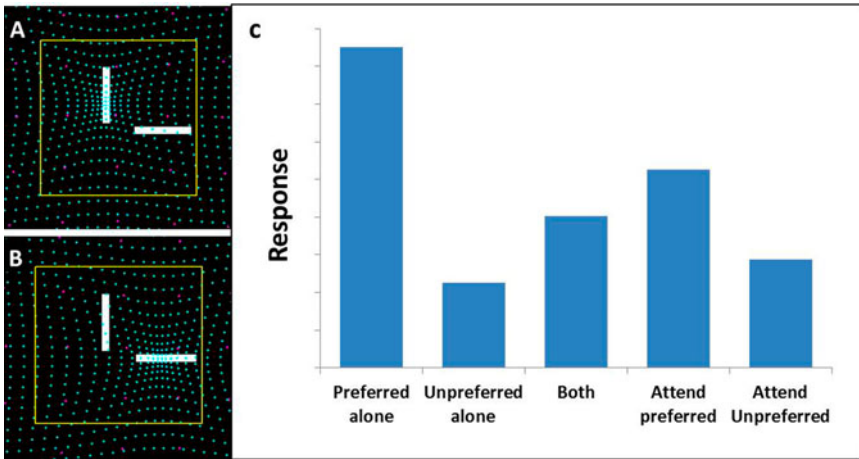


Figure 9. Biased competition: Two stimuli are presented in the RF of a second layer neuron whose preferred orientation is vertical. (A) Attention is focused on the preferred stimulus. (B) Attention is focused on the nonpreferred stimulus. (C) Simulated neuronal response matches that described in the literature—when one of the stimuli is attended, the neuronal response to the two stimuli is biased towards the response to that stimulus when presented alone. To view this figure in colour, please see the online issue of the Journal.

perpendicular to it (Figure 10). The simulated response to two stimuli in the RF, one eliciting a large response and another eliciting a small response, was in between the responses to these stimuli when placed alone in the RF. This is because the response of an L2 neuron was calculated as the average of its active afferents (see the “Neuronal activation” section in the Appendix for details). The important result, however, was the effect of attention. When attention was focused on any of the bars, the response of the neuron was biased towards its response when that bar was presented alone in its RF (Figure 9C). Thus, the simulation outcomes replicated the neurophysiological findings.

Enhanced spatial resolution

The attraction of RFs towards the centre of attention increases the overlap between RFs and increases the sampling density at the attended location (Figures 6 and 7), which could improve spatial resolution (e.g., Prinzmetal, 2005). We propose that in this sense attention acts as a transient emulation of the fovea, providing an attended peripheral location with a relative advantage despite not being at the centre of fixation. The high-density sampling zone at the attended location should lead to a higher spatial resolution at the focus of attention.

To test whether the AAF model indeed predicts a higher ability to resolve fine details with attention, we examined the neuronal responses of both layers, to a horizontal line containing a small gap (Figure 11A). The size of the gap was of a

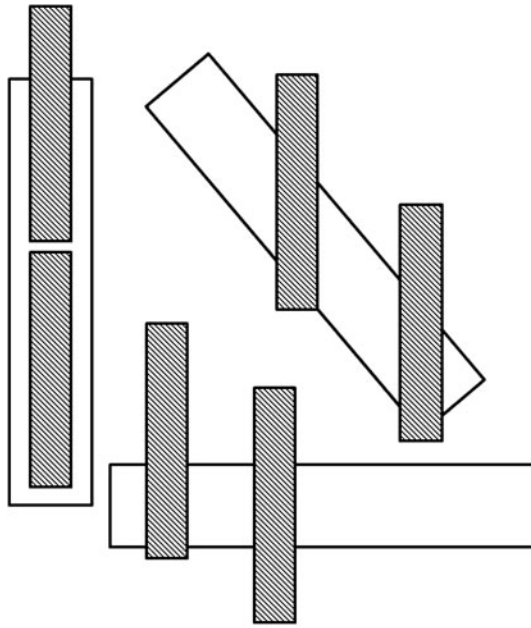


Figure 10. Elongated RFs: The figure demonstrates the relationship between elongated RFs (hatched vertical bars) and a rectangular bar stimulus at three different orientations. When the stimulus is oriented horizontally, it is always overlapped only by a fraction of an RF. The overlap increases when the angle between the orientation of the stimulus and the orientation of the RFs decreases, and is maximal when the stimulus is oriented vertically.

similar order of magnitude as the size of the L1 RFs. As described earlier, the response of L1 neurons was determined by a weighted sum of the luminance values in their RFs, and the response of L2 neurons was determined by the weighted sum of the activation levels of their L1 afferents (see Appendix for details). The simulated response to the line, of the second layer neurons, without attention (on the left) and with attention (on the right), is presented in [Figure 11B](#). Evidently, attention accentuated the gap. To test the generality of this outcome, the responses of first layer neurons whose RF falls within a rectangular zone embracing the stimulus were averaged at several points along the line. Attention in this simulation was directed to several locations along a vertical axis that passes through the gap. The averaged responses along the line are plotted in [Figure 11C](#). As can be seen, the difference between neuronal responses at the gap and those at neighbouring parts of the line is maximal when attention is directed to the centre of the gap and diminishes as attention is directed farther away. Note that the valley in the neuronal response corresponding to the gap in the stimulus is both wider and deeper with than without attention, increasing the likelihood that the difference in activation levels along the line is not a result of noisy response but of a real discontinuity in the

line. Therefore, the neuronal response differences at the gap demonstrated in [Figure 11](#) may underlie the ability to better resolve details with attention.

The finding that an attentional attraction of RFs towards the attended location enhances the ability to resolve small spatial details is in accordance with behavioural findings demonstrating that attention enhances the spatial resolution at the attended location (e.g., Yeshurun & Carrasco, 1998, 1999, 2000). These findings were typically linked to neurophysiological studies suggesting that attention contracts the cell's receptive field around the attended stimulus (e.g., Desimone & Duncan, 1995; Luck et al., 1997; Moran & Desimone, 1985).

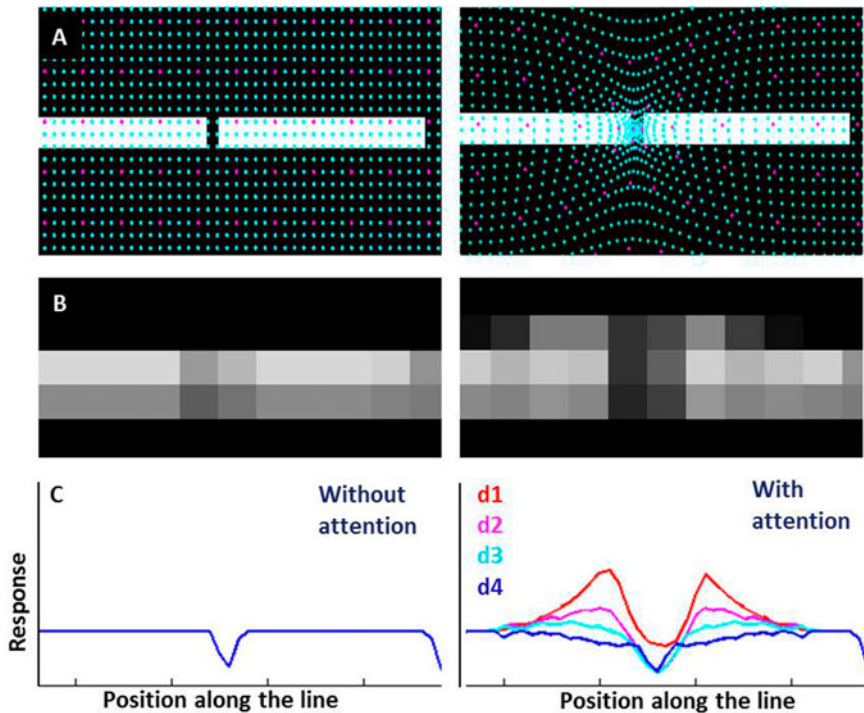


Figure 11. Enhanced spatial resolution at the focus of attention: (A) The stimulus—a horizontal line containing a small gap—overlaid by the centres of RFs, when attention is focused on the centre of the gap (right panel) or without attention (left panel). (B) The corresponding simulated neuronal response to the stimulus, of second layer neurons, under the two attentional conditions. (C) The responses of first layer neurons whose RF falls within a rectangular zone embracing the stimulus were averaged at several points along the line. Average response without attention is plotted on the left. The right panel displays the average response along the line when attention is focused at various distances from the centre of the gap (d1—the closest distance, d4—the farthest distance). Evidently, attention accentuates the gap: The difference between neuronal responses at the gap and those at neighbouring parts of the line is maximal when attention is focused at the centre of the gap and diminishes as attention is directed farther away. Hence, the high-density sampling zone, created by the attentional attraction field leads to a higher spatial resolution at the focus of attention. To view this figure in colour, please see the online issue of the Journal.

Particularly, it was suggested that attention enhances spatial resolution by effectively decreasing the average size of RFs at the attended location (e.g., Yeshurun & Carrasco, 1998, 1999). However, other studies observed that smaller RFs may lead to worse performance for example in localization tasks (e.g., Prinzmetal, 2005). The AAF model implies that shift of RFs towards the attended location—and the resulting higher sampling density—may underlie enhanced spatial resolution at that location. This new account does not contradict the original explanation of these behavioural findings, because, as demonstrated in Figures 1A and 2B, the shift of RFs in one layer can lead to the contraction of RFs in the next layer. Still, it suggests that the shift of RFs towards the centre of attention is the more fundamental account. Interestingly, we also simulated model responses when the attentional impact was the shrinkage of RFs instead of (or in addition to) the shift of RFs (using a Gaussian function to determine the amount of shrinkage, similar to the one used to determine the amount of shift). However, in comparison to RFs' shift, RFs' shrinkage added only a marginal contribution to the simulation of the previously mentioned attentional effects.

Perceptual distortions around the focus of attention

The layout of neurons in retinotopic visual areas of the cortex represents the spatial layout of the visual environment. Possibly, each neuron has some “position label” that relates neuronal activity to a location in space and enables to extract spatial information from neuronal activity. Under the assumption that this position label is fixed, shifts of receptive fields may distort perception. Anton-Erxleben, Henrich, and Treue (2007) examined this hypothesis and found indeed a perceptual enlargement of attended objects. This enlargement can be explained by the AAF model: The attentional attraction of RFs increases the number of neurons that respond to the attended stimulus, and assuming they still represent the preshift location, the corresponding “area of activation” is magnified (see Figure 4). A larger area of activation could be interpreted as indicating a larger stimulus. This magnifying effect may lead to additional perceptual distortions at the vicinity of the attended location (e.g., Fortenbaugh, Prinzmetal, & Robertson, 2011; Suzuki & Cavanagh, 1997). For instance it may underlie the repulsion effect—the finding that the perceived distance between a stimulus and a given location increases when this location is attended (e.g., Suzuki & Cavanagh, 1997). Specifically, Suzuki and Cavanagh (1997) found that when the brief presentation of a Vernier stimulus along the vertical meridian followed a cue stimulus that was flashed in one of the quadrants, the Vernier always appeared offset away from the cue. We repeated this setting with slight modifications: Figure 12 displays the simulation results of responses to a Vernier stimulus when the segments of the stimulus are aligned horizontally (top panel) or misaligned (bottom panel). When attention was directed to a location above the left segment, the attraction of RF centres to this location led to a repulsion effect: Neurons that

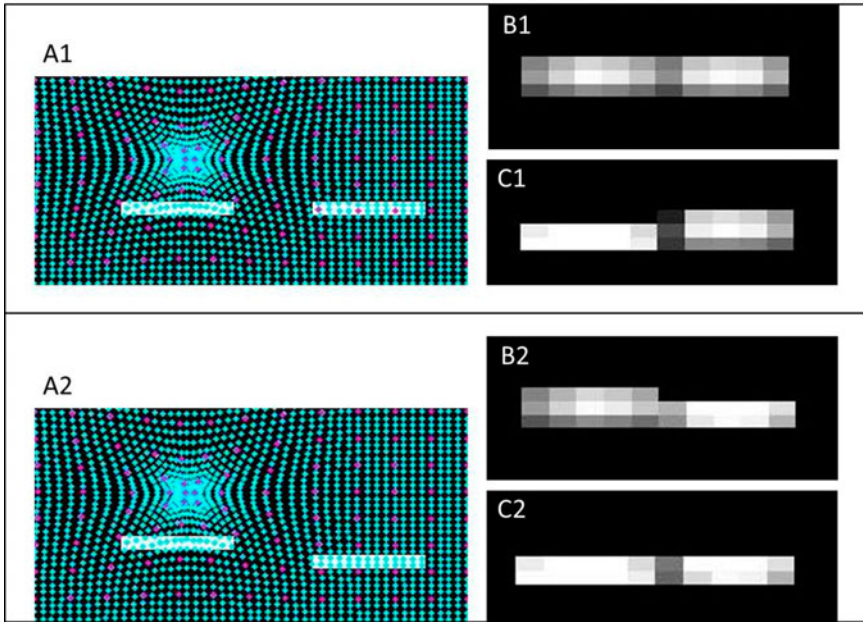


Figure 12. Simulated repulsion effect. Left column displays two Vernier stimuli: In the top panel (A1) the segments of the Vernier are aligned (Suzuki & Cavanagh, 1997), whereas in the bottom panel (A2) they are not. The stimuli are overlaid by the centres of RFs when attention is directed to a location above the left segment. The right column displays the response of L2 neurons to the stimulus. In each panel, the top row (B1 and B2) displays responses to the stimulus without attention and the bottom row (C1 and C2) displays the responses when attention is allocated as demonstrated in the figure. Attention evokes a repulsion effect and thus, with attention, the response to the aligned segments becomes misaligned (top panel), and the response to the misaligned segments becomes aligned. To view this figure in colour, please see the online issue of the Journal.

responded to the left segment corresponded to RFs that were more distant from the attended location (without attention) and therefore their alignment with the neurons that responded to the other segment was modified, confirming with the study of Suzuki and Cavanagh. Note also how attention improved the separation between the segments in the responses of L2 neurons. This is consistent with the finding (Yeshurun & Carrasco, 1999) of higher Vernier acuity with attention.

TEMPORAL ASPECTS OF THE ATTENTIONAL ATTRACTION FIELD

Clearly, a comprehensive view of the visual perceptual system requires understanding of how we process both the spatial and temporal aspects of the visual stimulus. Yet we know much more about the former than the latter. This is especially true of spatial attention. Although recently there is growing interest in

modulations of temporal aspects of perception brought about by spatial attention (e.g., Rolke, Dinkelbach, Hein, & Ulrich, 2008; Visser & Enns, 2001; Yeshurun & Marom, 2008), previous models of attention were typically developed to account for attentional effects in the spatial domain, and they rarely dealt with the complementary temporal facet. In contrast, based on the attentional attraction and on the variability in neuronal responses, the AAF model can also account for temporal effects.

The attraction of RFs increases the number of neurons that respond to a stimulus as well as the activity of individual neurons (see Figure 4). Therefore, with attention, a (weighted) summation of the temporal response functions of the individual neurons will produce a joint response with higher amplitude. A higher neuronal response to a stimulus corresponds to a higher signal-to-noise ratio. This is especially substantial at the extremities of the temporal response (i.e., when the response starts to rise and/or near the end of its decay when it is about to return to baseline), where without attention the response may be too weak to lead to perception. Furthermore, it is known that there is variability in the response of any single neuron in all parameters of the response function (e.g., amplitude, duration, onset time following stimulus onset, etc.). The larger population that responds to the stimulus with the attentional attraction of RFs, accompanied by this inherent variability of the individual neurons in response onset and in response duration, increases the probability that the joint response will be wider with attention (see Appendix for details). This phenomenon is unique to the AAF model. Thus, with attention the AAF model will induce on average a joint (L2) response that rises sooner, lasts longer and decays later (Figure 13). This result can account for a host of psychophysical effects of spatial attention in the temporal domain.

To demonstrate the ability of the AAF model to account for such attentional effects, we extended the response of our simulated neurons over time using the temporal impulse response (TIR) function (e.g., Burr & Morrone, 1993). The amplitude of the TIR of a neuron in both layers was determined by the same spatial summation function employed to evaluate the spatial aspects of the AAF (thus, the amplitude achieved the same value as the neuron's activation level). Variability of the neuronal response onset of L1 neurons was modelled by using normally distributed response start times relative to stimulus onset. Note that the response of an L2 neuron is the joint TIR of its afferent neuronal population. (A mathematical formulation of the TIR implementation is included in the Appendix.)

Prior entry

Figure 14A displays the simulated TIR of an L2 neuron to a single brief stimulus in its RF with and without attention. The results show that the attended TIR rises faster than the nonattended TIR. A population response function that rises sooner

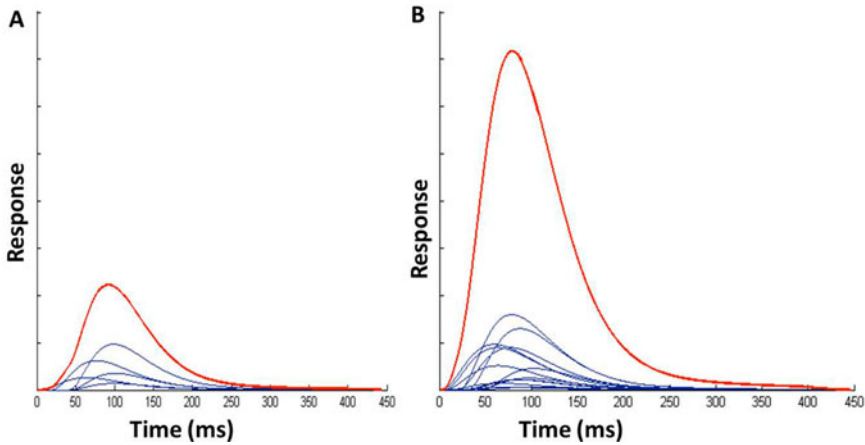


Figure 13. Temporal response functions of individual neurons (blue curves) and the joint population response function (red curve) (A) without attention (B) with attention. With attention more neurons respond, with higher amplitude (in average) and a larger variability which leads to a wider population response, rising faster and decaying later than without attention. The joint response is determined by a weighted summation function. To view this figure in colour, please see the online issue of the Journal.

may underlie the phenomenon of prior entry reported by several studies (e.g., Enns et al., 1999; Shore et al., 2001). These studies have found that a stimulus presented at the attended location was perceived before a stimulus presented at an unattended location. This finding was typically interpreted as an indication of a faster processing rate with spatial attention (e.g., Shore et al., 2001). Faster processing rate with spatial attention was also demonstrated with the visual search and speed–accuracy tradeoff paradigm (Carrasco & McElree, 2001). Since a neuronal response that rises faster should lead to an earlier perceptual experience, the AAF model is in line with this interpretation (e.g., McDonald, Teder-Salejarvi, Di Russo, & Hillyard, 2005).

Prolonged perceived duration and prolonged temporal integration

As can be seen in Figure 14A, the attentional attraction leads also to a slower decay of the TIR function. The faster rise of the population response function and its slower decay may underlie the finding that the duration of attended stimuli seems longer than that of nonattended stimuli (e.g., Enns et al., 1999; Mattes & Ulrich, 1998; Yeshurun & Marom, 2008). It is typically believed that the perceived duration of an event depends on the number of pulses counted by an internal counter before the response to the event decays (e.g., Thomas & Weaver, 1975; Treisman, 1963; Tse, Rivest, Intriligator, & Cavanagh, 2004; Ulrich, Nitschke, & Rammsayer, 2006). If the internal response to an attended event lasts longer (Enns et al., 1999; Mattes & Ulrich, 1998, Yeshurun &

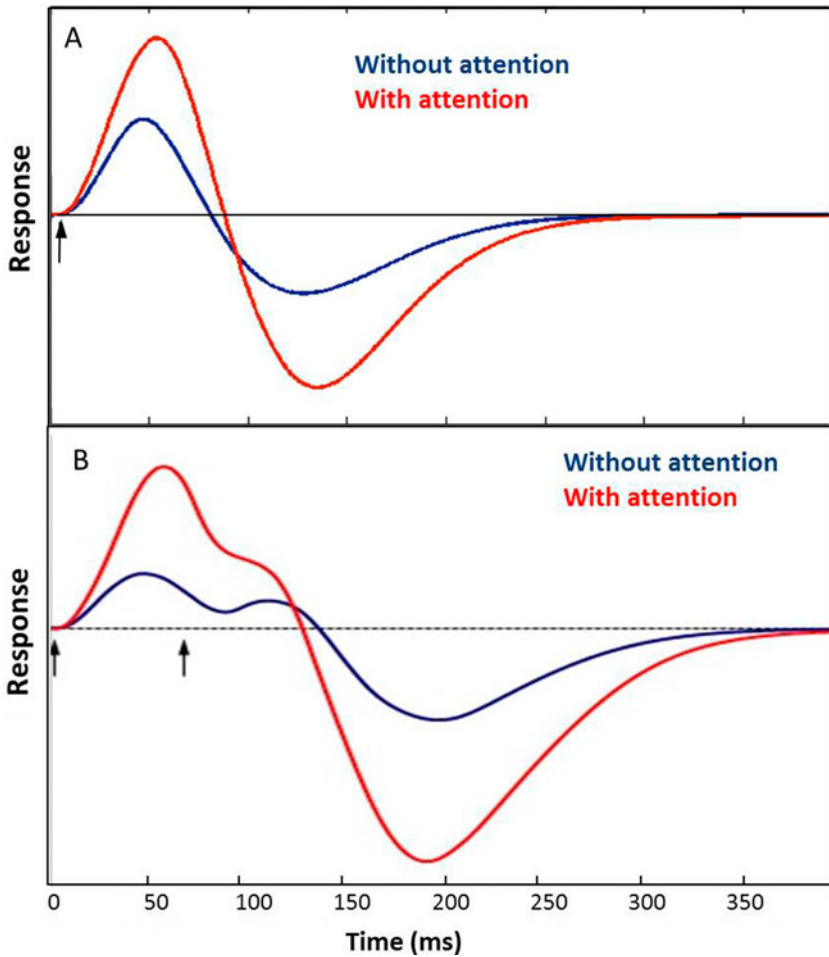


Figure 14. Temporal effects of the attentional attraction field: (A) An example of a simulated response of an L2 neuron to a brief stimulus—a single pulse in its RF, with and without attention, as a function of time (the arrow indicates stimulus onset). The attentional increment of the number of L1 neurons that respond to the stimulus and the enhanced activity of individual neurons increase both the variability of the joint neuronal response and its amplitude. This often results in a wider response: a response that rises sooner and decays later. (B) An example of a simulated response of an L2 neuron to two pulses presented successively at the same location in its RF, with and without attention. The pulses are separated by a 70 ms interval. The arrows indicate the pulses' onset. Because attending a single pulse results in a wider neuronal response, when the two pulses are attended the summed responses tend to merge, rendering the two pulses less separable. Such a merged neuronal response may underlie the psychophysical finding that attention degrades the ability to resolve rapid changes in light intensity over time. To view this figure in colour, please see the online issue of the Journal.

Marom, 2008), more pulses will be counted during the attended event and its duration should indeed be perceived as longer. A slower decay of the population response function with attention suggests also that attention should prolong our ability to integrate information over time. This prediction is consistent with a recent study demonstrating, using the Classification Images technique that the deployment of transient spatial attention results in a larger temporal integration window (Megna, Rocchi, & Baldassi, 2012).

Diminished temporal resolution

We also examined the simulated response of an L2 neuron to a two-pulse stimulus (i.e., a stimulus composed of a successive presentation of two brief flashes) in its RF. As can be seen in Figure 14B, when the two pulses are attended the summed responses tend to merge, rendering the two pulses less separable. We further simulated the neuronal response to a two-pulse stimulus with a variable SOA (stimulus-onset asynchrony—the time between the onset of first and second pulse) and counted the number of peaks of the neuronal response curve in each SOA condition (see Appendix for details). Figure 15 includes an example of the outcome of 1000 iterations per SOA. It is evident that the peaks corresponding to the two onsets are merged into a single peak more often with attention. Such a merged neuronal response implies a deteriorated

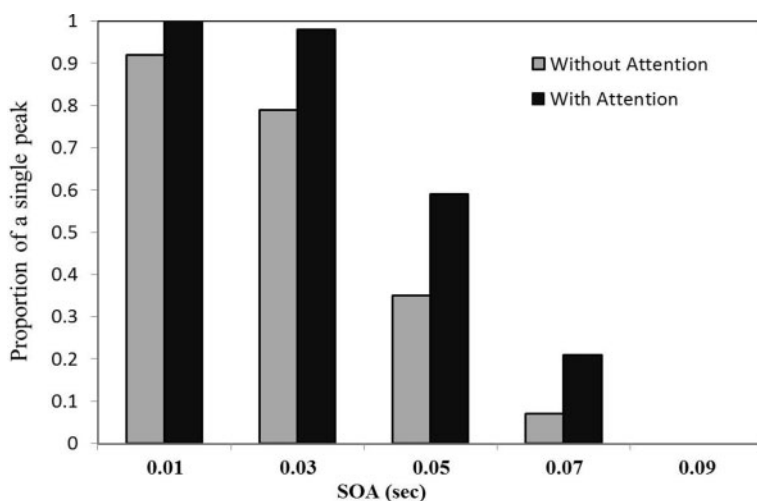


Figure 15. The results of simulating L2 neuronal responses to a two-pulse stimulus with a variable SOA: The simulation consisted of 1000 iterations per SOA and the bars indicate the proportion of cases in which a single activity peak was counted, as a function of the attentional condition and the SOA. Attending the location of the two pulses resulted more often in a merged response (i.e., a response that includes only a single peak).

ability to resolve the temporal gap between the two presentations. Hence, this is consistent with the finding that spatial attention impairs temporal resolution at the attended location (e.g., Hein et al., 2006; Rolke et al., 2008; Yeshurun & Levy, 2003). Specifically, these modulations of the attended TIR may underlie the psychophysical finding that observers' ability to indicate whether a target is flickering (i.e., composed of two pulses) or continuous (i.e., composed of one pulse) is diminished when attention is directed in advance to the target location (e.g., Rolke et al., 2008; Yeshurun, 2004; Yeshurun & Levy, 2003).

It is important to note that the variability in response onset was implemented similarly in both attentional conditions (i.e., with and without attention) and that the only attentional modulation that was implemented in the model was the attraction of RFs to the attended location. As already described, this attraction results in a larger neuronal population that responds to the stimulus, leading to a higher variability and overall increased activation amplitude of the population response function, producing on average a response that rises sooner, lasts longer and decays later. Thus, the simulations show that the same mechanism that accounts for spatial effects of attention—the attraction of RFs to the attended location—can also account for temporal effects of attention.

DISCUSSION

An important unsettled issue concerns the nature of the attentional mechanism. Here we presented a feed-forward model in which the attentional mechanism was portrayed as an attraction field and demonstrated that the mere attraction of RFs towards the focus of attention can explain a wide range of attentional effects. By this model the attraction of RFs towards the focus of attention propagates up the visual hierarchy and may lead to changes in the structure and position of RFs of subsequent, higher layers. Most importantly, the AAF can account for an attentional gain modulation: increased neuronal response at the attended location. This means that previous results that were obtained assuming gain modulations remain applicable. The attraction of RFs towards the focus of attention can account for spatial effects of spatial attention—the Mexican hat profile of the attentional modulation, enhanced spatial resolution at the attended location, biased competition, and perceptual distortions such as perceptual enlargement of attended stimuli and the repulsion effect. It can also account for temporal effects of spatial attention—the degradation of temporal resolution, prior entry, prolongation of perceived duration and prolongation of temporal integration. Thus, the mere attraction of RFs towards the focus of attention can provide a simple account for a host of attentional phenomena. None of the previous models of attention can account for all of the effects of attention that are accounted for by the AAF model. Given that attention consists of multiple independent but interactive systems, it is reasonable to assume that this mechanism is not the only

mechanism operating when attention is drawn to a specific location. Still, the fact that attentional attraction of RFs can explain such a large number of attentional phenomena suggests that this mechanism may play a central role.

On a more conceptual level, the attraction of RFs towards the attended location may be considered as a recruitment of processing resources. The idea that the deployment of attention is analogous to resource allocation prevails in the literature (e.g., Duncan, 1980; Kahneman, 1973; Kerr, 1973; Navon & Gopher, 1979; Norman & Bobrow, 1975). The AAF model offers a straightforward instantiation of the attentional recruitment of resources: With attention more neurons are available to process a stimulus. It was previously suggested that the shift of RFs towards the focus of attention is a recruitment of resources (e.g., Suzuki & Cavanagh, 1997; Womelsdorf et al., 2006), but the AAF model suggests that this is the fundamental impact of attention. All other effects are an indirect consequence.

Model predictions

A central prediction of the AAF model is that the shift of RFs towards the centre of attention is related directly to the diameter of the attended area and inversely to the distance of the RF from the centre of attention. We have suggested a Gaussian attraction field, which seems biologically plausible, but other options are possible of course. This fundamental prediction may be measurable in various ways (e.g., Kosovicheva, Fortenbaugh, & Robertson, 2010). For example, single cell recordings may provide information regarding the magnitude of the shift as a function of the distance from the focus of attention. According to our model a nonlinear relationship may prevail (e.g., Gaussian).

The model includes several parameters that influence the behaviour of individual neurons and consequently the overall behaviour of the neuronal population. A central one is σ , which represents the diameter (or concentration) of the attentional focus. For example, the value of σ affects the shape of the Mexican hat distribution of RFs (Figure 7). Assuming a Gaussian attraction field, when σ is small (attention is narrowly focused) the attentional influence is expected to be accentuated. Specifically, the enhancement at the centre of attention is expected to increase. A similar idea was presented by Eriksen and St. James (1986) in their “zoom-lens” model of attention, by which as the size of the attentional field increases, the density of the processing resources within the field decreases. This idea was further supported by Müller and colleagues (Müller, Bartelt, Donner, Villringer, & Brandt, 2003), who demonstrated that, as the size of the attended region increased, the extent of activated retinotopic visual cortex also increased, but consistent with the idea of limited resources, the level of neural activity in a given subregion decreased. Another consequence of a small σ , according to the AAF model, is that the suppression at the surrounding annulus of attention is expected to be deeper and wider. When σ gets larger (a

broader spread of attention) the depression of the density function is expected to become shallower and narrower. By manipulating the spread of attention (and hence manipulating σ) these predictions can be tested both with behavioural methods that indirectly assess the Mexican hat shape of the attentional modulation, as well as physiologically.

The model additionally predicts that the magnitude of the attentional effect on the response of a given neuron depends on the change in the spatial relationship between the stimulus and the neuron's RF, resulting from the shift of the RF towards the focus of attention. This shift may lead to an increase in the portion of the RF that overlaps the stimulus and accordingly to an enhanced response. Importantly, however, there may be cases when a neuron's response is not affected by attention because the spatial relationship between the neuron's RF and the stimulus is not affected by the attentional shift (e.g., when there is full or no overlap under both attentional conditions—[Figure 3](#)) and even cases when the attentional shift may lead to a decrease in the portion of the RF that overlaps the stimulus and hence to a decrease in the neuron's response (e.g., with stimuli whose shape is irregular—[Figure 5](#)). To our knowledge, this is a unique prediction.

Model limitations

An important and fundamental issue is the feed-forward nature of the AAF model. One might wonder how such an attentional mechanism might be physiologically implemented. We do not offer speculations at this time. Our main goal, at this point, was to demonstrate the merit of the idea that the most fundamental impact of attention is the attraction of receptive fields to the focus of attention.

For the sake of demonstrating the relevance of the attentional attraction field we have made many simplifying assumptions. For instance, all RFs of a given layer were modelled as identical rectangles (i.e., we did not deal with issues of eccentricity, assuming a constant size and density of RFs). We also modelled only two layers: the layer on which attention is operating directly (L1) and the one influenced indirectly (L2). Applying the attentional attraction also to L2 would emphasize the results. Of course, additional layers could easily be added to the model to represent the layered structure of the visual hierarchy in the biological visual system. Additionally, the simulations presented here were generated without normalization processes; however, preliminary tests suggest that the addition of such processes would not make a qualitative difference. In addition, the version of the AAF model that is discussed here only simulates spatial attention and does not deal with feature-based attentional effects as do some of the previous models (e.g., Boynton, 2005; Lee & Maunsell, 2009; Reynolds & Heeger, 2009; Treue & Martinez-Trujillo, 1999).

The magnitude of perceptual distortions resulting from attention, as reported in the literature, is relatively small. For example, changes in perceived size (e.g., Anton-Erxleben et al., 2007) were typically less than 15%. In contrast, the results of the model simulations presented in this paper should lead to perceptual distortions that are much larger (see Figure 4). The specific selection of parameters in the simulations was not meant to quantitatively match reported effect sizes but rather to emphasize the attentional effects for demonstrational purposes; however, in future work it would be interesting and worthwhile to exploit behavioural findings (e.g., the change magnitude in perceived size and the magnitude of the shift in perceived location in the repulsion effect; Suzuki & Cavanagh, 1997), as constraints on parameter values. Values that replicate the size of the simulated effects may be used to produce quantitative predictions and provide further insight into the underlying processes.

Another issue that was not addressed directly in the model is the distinction between voluntary and involuntary attention. Some of the effects that were simulated by the model (e.g., changes in location and size of receptive fields and enhanced neuronal responses at the focus of attention) were found in studies that used single-cell recordings in monkeys that were instructed to attend to a stimulus. Other effects (such as perceptual distortions at the focus of attention) were obtained using involuntary reflexive attention. Other effects yet (e.g., the Mexican hat profile of attention, enhanced contrast sensitivity, and enhanced spatial resolution) were found both with involuntary and voluntary attention. There is a controversy in the literature whether the processes underlying these types of attention are separate (e.g., Awh, Belopolsky, & Theeuwes, 2012; Carrasco, 2011; Gibson & Kingstone, 2006; Klein & Shore, 2000; Ristic & Kingstone, 2012; Schreij, Los, Theeuwes, Enns, & Olivers, 2013). The model does not provide a clear answer to this debate. It is true that the effects were all simulated using the same procedure; however, it is possible that a single mechanism—the one responsible for the shift of receptive fields towards the focus of attention—is evoked by different processes.

Finally, the AAF model only refers to processes that occur once attention is already focused at the selected location. It does not handle prior processes that lead to that selection (see Itti & Koch, 2001, for a review of models that consider prior selection processes).

Future work should explore possible mechanisms underlying the attentional attraction field, and test more complex versions of the model as well as its applicability to additional attentional phenomena.

To conclude, we have demonstrated that a single attentional mechanism— attracting the centres of RFs towards the focus of attention—can account for a diverse range of attentional modulations, linking physiological measurements at the unit level with behavioural observations of both the spatial and temporal domains of perception.

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APPENDIX

Definitions

Let L_0 denote the two dimensional stimulus field (SF).
 $a(L_0(x, y)) = L_0(x, y)$ —the stimulus intensity at (x, y) .
 $L_k(n_1, n_2)$ —an element (neuron) of the two dimensional L_k layer. $k = 1, 2$.
 $a(L_k(n_1, n_2))$ —the activation level (response) of $L_k(n_1, n_2)$.
 $inp(L_2(n_1, n_2))$ —the fixed rectangular zone of L_1 that provides input to $L_2(n_1, n_2)$.
 $inp(L_1(n_1, n_2))$ —the rectangular zone of L_0 (SF) that affects $L_1(n_1, n_2)$. Unlike the fixed input zone of an L_2 neuron, the input zone of an L_1 neuron changes dynamically with attention.
 The RF of an L_1 neuron equals by definition to its input zone:

$$RF(L_1(n_1, n_2)) = inp(L_1(n_1, n_2))$$

The RF of an L_2 neuron is the union of the RFs of the neurons in its input zone:

$$RF(L_2(n_1, n_2)) = \bigcup_{ij} RF(L_1(i, j)), L_1(i, j) \in inp(L_2(n_1, n_2))$$

Neuronal activation

The activation level of a neuron was calculated by spatial summation as follows:

$$a(L_k(n_1, n_2)) = \left[\sum_{ij}^{d_1, d_2} w(i, j) a(L_{k-1}(i, j)) \right]_T, L_{k-1}(i, j) \in inp(L_k(n_1, n_2)), k = 1, 2$$

where w is a weight function that is applied to $inp(L_k(n_1, n_2))$. The size $d_1 \times d_2$ was set to equal the size of $inp(L_k(n_1, n_2))$. Thus, the activation of an L_1 neuron was calculated as the weighted sum of the intensity values within its RF. The activation of an L_2 neuron was calculated as the weighted sum of the responses of its “afferent neurons”.

$[\]_T$ denotes thresholding: $[A]_T = \max(A - T, 0)$.

Several weight functions were tested:

- (1) summation: $w(i, j) = 1, \forall i, j$
- (2) averaging: $w(i, j) = 1/(d_1 \cdot d_2), \forall i, j$
- (3) Gaussian weighted averaging: a rotationally symmetric Gaussian mask of size $(d_1 \cdot d_2)$, with σ set to be $\max(d_1, d_2)/2$.

$$h_g(i, j) = e^{-(i^2 + j^2)/(2\sigma^2)}$$

$$w(i, j) = \frac{h_g(i, j)}{\sum_i \sum_j h_g}$$

There was no substantial difference between the various weight functions with respect to the results reported in the main paper. The figures in the paper were produced using the Gaussian weighted averaging for the activation of L_1 neurons (e.g., Compte & Wang, 2006; Womelsdorf et al., 2008).

The response of L2 neurons was computed using an activation dependent averaging:

$$w(i, j) = 1/p, \forall i, j, \text{ such that } P = \sum_{i,j}^{d_1, d_2} [a(L_1(i, j)) > T]$$

This function takes into account the size of the active afferent population.

The Attentional Attraction Field (AAF)

The shift that was induced by the attentional attraction on an RF was determined using a Gaussian function. Given an RF whose centre is r units distant from the centre of attention, the Gaussian function, $G(r, \sigma)$, determines the proportion of r by which the RF centre is shifted towards the centre of attention. The RF's shift is thus:

$$\text{shift}(r, \sigma) = r \cdot G(r, \sigma) = r \cdot \frac{\exp(-0.5r^2/\sigma^2)}{\sigma\sqrt{2\pi}}$$

σ represents the diameter of the attentional focus and was restricted to values larger than 0.4. This number was chosen to warrant a proportion of r that is bounded by 1, and can be viewed as representing a lower bound of the ability to focus attention (e.g., Eriksen & Hoffman, 1972; Murphy & Eriksen, 1987).

Note that other bell-shaped functions could be used to define the attentional attraction field yielding similar results (specifically, we also tested a cosine attraction field).

RFs' density function

We calculate here $RD(r)$, the relative density of the RFs after applying attention, with respect to $\rho(r)$, the density of the RFs prior to the application of attention. The density of RFs is defined as the number of RFs per unit of distance, along a radial axis centred at the focus of attention. It is assumed that prior to the application of attention the RFs are distributed uniformly. Let us define $\rho(r) = 1$.

The distance $r_a(r, \sigma)$ of an RF centre from the centre of attention, after applying the attentional attraction is given by

$$r_a(r, \sigma) = r - \text{shift}(r, \sigma) = r - r \cdot G(r, \sigma)$$

The relative density of RFs after applying the attentional attraction is therefore:

$$RD(r) = \frac{1}{\frac{d}{dr}r_a(r, \sigma)} = \frac{1}{\frac{d}{dr}(r - r \cdot G(r, \sigma))} = \frac{1}{1 - (1 - \frac{r^2}{\sigma^2})G(r, \sigma)}$$

As can be seen in Figure 7, this function has the shape of the positive portion of a Mexican hat centred at (0,0). The computational simulation produced a similar pattern of RFs' density around the focus of attention.

Temporal aspects of neuronal activation

The Temporal Impulse Response function (TIR). The temporal response of a neuron to a brief stimulus in its RF can be modelled by a function of four positive parameters (e.g., Burr & Morrone, 1993), a_0, a_1, a_2, a_3 :

$$TIR(t) = a_0 H(t) \cdot t \cdot \sin(2\pi(a_1 t(t+1)^{-a_2})) \exp(-a_3 t)$$

$$H(t) = \begin{cases} 0 & t < 0 \\ 1 & t \geq 0 \end{cases}$$

where t is time measured from stimulus onset. a_0 determines the amplitude of the function—or the

overall gain, a_1 determines the fundamental frequency of oscillation, a_2 determines the modulation of frequency over time, and a_3 determines the steepness of the exponential decay.

TIR implementation parameters. We employed function parameters that were previously reported in the literature (Burr & Morrone, 1993) with the following modifications:

- (1) The amplitude of the TIR function— a_0 —was determined by the value of the calculated spatial summation as described in the Neuronal activation section in this Appendix.
- (2) We varied the delay of response onset ($\delta_t \geq 0$) to the stimulus onset.

Thus, the temporal response function was modelled as $TIR(t')$ such that $t' = t - \delta_t$ for $t \geq \delta_t$ and 0 otherwise.

We tested two distributions of response onset delay: (a) a uniform distribution:

$\delta_t \sim U(t_0, t_1)$ for some t_0, t_1 . (b) a normal distribution: $\delta_t \sim N(\mu, \sigma^2)$ for some σ and μ , considering only the positive values of the distribution. The simulation outcomes displayed here were obtained using the normal distribution, but similar results were obtained using a uniform distribution.

TIR summation. Let $TIR(L_1(i, j), t)$ represent the temporal response of a neuron in the first layer. The joined TIR of the neuronal population in a RF of an L2 neuron was calculated as a weighted sum of the individual TIRs as follows:

$$TIR(L_2(n_1, n_2), t) = \left[\sum_{i,j}^{d_1, d_2} \sum_t w(i, j) \cdot TIR(L_1(i, j), t) \right]_T$$

such that $L_1(i, j) \in inp(L_2(n_1, n_2))$.

The width of the temporal response. Let response onsets of individual neurons be drawn from some distribution D , and let $p(early)$ be the probability that the onset of a response to a stimulus, t_{onset} , is sooner than some t_{early} time units.

$$p(early) = p(t_{onset} < t_{early})$$

In a population of n neurons that respond to the stimulus, the probability $Pn(k.early)$ to find k active neurons before t_{early} is given by:

$$Pn(k.early) = \binom{n}{k} p(early)^k q^{n-k}, q = 1 - p(early)$$

Similarly, let $t_{duration}$ be the duration of a response, and $p(late)$ the probability to find a neuron still active after t_{late} time units from stimulus presentation.

$$p(late) = p(t_{onset} + t_{duration} > t_{late})$$

The probability $Pn(k.late)$ to find k active neurons after t_{late} is

$$Pn(k.late) = \binom{n}{k} p(late)^k q^{n-k}, q = 1 - p(late)$$

Clearly, when the size of the active population is larger, both $Pn(k.early)$ and $Pn(k.late)$ are larger; therefore, with attention, when more neurons respond to a stimulus, there is a higher probability to have a joint response function that is temporally wider.

In the model simulations we used a fixed value for the duration of a response. A response duration that is also randomly drawn from some distribution would further increase the difference in response width between the attentional conditions.

Detecting local maxima in the neuronal temporal response curve. We simulated the neuronal response to a two-pulse stimulus with a variable SOA and counted the number of peaks in the neuronal response curve (without any smoothing) in each SOA condition. Peak detection was carried out by a liberal algorithm: A negative derivative of the response curve immediately following a nonnegative derivative was considered as local maxima (peak).

Formally, the derivative of the response curve at t was defined as:

$$\frac{d}{dt} TIR(t) = TIR(t) - TIR(t - 1), t > 0$$

Figure 15 presents the proportion of cases in which a single peak was detected, in each attentional condition.

Simulation parameters

Most of the parameters that were used in the model were chosen arbitrarily and modified dynamically as part of the test phase of the model. Although different parameters led to different quantitative results, the observed phenomena were replicated. For the sake of this paper the following parameters were selected:

Stimulus field (SF). A 256×256 matrix. The spacing between the pixels was defined to be representing 0.1° . In all simulations the background was black and the stimuli were homogeneous grey (medium contrast) or white (high contrast).

Visual hierarchy (VH). The layers in the VH were determined by two parameters: (a) the size of the receptive fields of neurons in the layer, and (b) the spacing between RF centres. Without attention, all RFs had the same size and the spacing was uniform. The values that were used in all the simulations described in this paper (apart from the simulation of “biased competition”—see later) were:

- Layer 1: RF spacing was 4 pixels; RF size was a 7×7 matrix of SF pixels.
- Layer 2: RF spacing was 16 pixels; RF size was a 7×7 matrix of L1 neurons which is equivalent to a 31×31 matrix of SF pixels;

Base activity of the neurons in both layers was defined to be null (0). Testing the model with a random baseline activity did not alter substantially the simulation results.

Attentional modulation of RFs. The parameter σ that defines the concentration of attention was set in some simulations to 0.4° and in others to 0.6° ; again, the exact value does not qualitatively change the simulations' outcome.

Neuronal activation. As described in the “Neuronal activation” section earlier in the Appendix, response amplitude was calculated by a weighted summation function followed by thresholding. In the simulations presented in this paper, the threshold was always set to 0.

Next is a summary of the specific implementation details of the various simulations. Note—receptive field sizes are reported in the “no attention” condition. Size and location values are in SF pixels. Locations are relative to the top-left corner of the SF matrix. Unless otherwise stated, the parameter σ , defining the concentration (radius) of attention, was set to 0.4° .

Induced changes in location and size of RFs. In this simulation, the radius of attention, σ , was 0.6° . No stimulus was used. The centre of the L2 RF was at (32, 32) from the top-left corner of the SF matrix and its size was 25×25 pixels. In the “inside” condition, attention was focused at (30, 30) and in the “outside” condition at (54, 30).

Enhanced response. In this simulation the stimulus was a 9×9 high contrast (brightness value 255) square. Attention was directed to its centre.

The Mexican hat profile of attentional modulation. Two 6×6 square stimuli with medium contrast (brightness—128), were placed in the SF aligned horizontally. The top-left corner of the left one was at (69, 97) and of the right one at (101, 97). Attention was centred on the rim of the right stimulus at (101, 100) with σ set to 0.6° . The RFs of the recorded L2 neurons were centred at (64, 96) and at (96, 96), respectively.

Biased competition. RFs in this simulation differed from RFs in other simulations. To enable orientation selectivity, L1 RFs were elongated vertical rectangles of 3×17 SF pixels. The distance between RF centres of L1 neurons was 3 pixels. In order to accommodate two stimuli, the size of L2 RFs was larger than in other simulations. It was a matrix of 16×16 L1 neurons (48×62 SF pixels). The stimuli were two similar high contrast (brightness—255) bars, one vertical (2×16) and one horizontal (16×2). The top-left corner of the vertical bar was placed at (92, 82) and that of the

horizontal bar, at (101, 99). Attention was centred at (92, 92), (107,100) and (140,100) in the “attend preferred”, “attend nonpreferred”, and “attend away” conditions, respectively, with σ set to 0.6° . The RF of the L2 recorded neuron was centred at (100,100). Simulations with larger stimuli (e.g., 10×20 SF pixels) yielded similar results. Simulations using other orientation selectivity methods, such as using edge detectors, yielded similar results.

Enhanced spatial resolution. In this simulation the stimulus was a medium contrast (brightness—100) horizontal long line (170×10). Its top-left corner was at (21, 95). The width of the gap was 5 pixels, starting from x-coordinate 100. Attention was directed to four locations: (101,100), (101, 95), (101, 90), and (101, 85).

Perceptual distortions around the focus of attention—the repulsion effect. The simulation used two medium contrast (brightness value—128) Vernier stimuli. Each stimulus was composed of two horizontal segments of 50×8 pixels. In the aligned condition the top-left corner of the left segment was at (55, 91) and of the right one at (140, 91). In the misaligned condition the top-left corner of the right segment was at (140, 102). Attention was directed to (84, 65), above the left segment.

Temporal effects. In addition to the parameters controlling the shape of the TIR function, described earlier, the model includes a parameter that controls its duration. In the simulations reported in this paper, duration of the TIR response was 0.4 s.

Response onset was drawn from a normal distribution, $N(\mu, \sigma^2)$, where μ was at stimulus onset and σ was 0.04 s. Only the positive half was used.

The stimulus in these simulations was a medium contrast (brightness—130) small square (3×3) centred at (100×100). Attention was directed to the centre of the stimulus. The RF of the recorded L2 neuron was centred at (96, 96).