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The spotlight of attention: shifting, resizing and splitting receptive fields when processing visual motion

Neurons in the visual cortex as hard-wired filters for spatial and non-spatial stimulus properties

At all levels of the visual system of primates, from the retina to higher levels of processing in extrastriate cortex, neurons change their activity, i.e., their rate of action potentials, when visual stimuli are presented within a specific, circumscribed region of visual space. This *receptive field* (RF) of each neuron is an essential physiological property that acts as a spatial filter, shaping the encoding of visual signals. Since the seminal work of Hubel and Wiesel in the 1960s (e.g., [7]) electrophysiological methods in non-human primates have been continuously refined to determine the location and shape of RFs for neurons throughout the visual cortex. Such studies have revealed a basic organization of the primate visual system in which the image of an organism's environment projected onto the retina is encoded by neurons in a multitude of areas in the striate and extrastriate visual cortex, each containing retinotopically organized maps created by the systematic tiling of the visual field by the RFs of neighboring neurons. The size of the RFs increases with eccentricity as well as along the processing hierarchy, from the striate to extrastriate cortex, until they become so large that they cover most or all of the visual field captured by the eyes.

The spatial tuning embodied by a visual neuron's RF is combined with a tuning for non-spatial features, i.e., a systematic selectivity for one or several non-spatial stimulus properties. For example, neurons in area V4 in the temporal processing pathway of the visual cortex show tuning for the orientation and color of a stimulus inside their RF, while neurons in the middle temporal area of the superior temporal sulcus (area MT of the dorsal processing pathway) are tuned for the direction and speed of visual motion, as well as the stimulus' stereoscopic disparity.

Importantly, the predominant and long-held view was that all the way from striate to extrastriate visual cortex the spatial structure of the neurons' RF, as well as their non-spatial tuning are hard-wired properties. Such invariance would provide an invariant "labeled line code" for the location and other basic aspects of a stimulus, unaffected by top-down factors such as the stimulus' behavioral relevance.

Changing a neuron's relative sensitivity to multiple stimuli inside the receptive field

In 1985, Moran and Desimone [14] challenged this view for areas in the ventral cortical processing pathway when they made an interesting observation. They positioned two oriented bars (one with the preferred and one with a less preferred orientation) inside the receptive field of a neuron in area V4 of rhesus monkeys trained in an attentional task and observed that when the animals directed their attention to one of the stimuli, the neurons increased their responses when attention was on the preferred stimulus (i.e., the one producing a strong response) and reduced their response when attention was on the less preferred stimulus (i.e., the one that produced a weaker response). This effect seemed to indicate a reduced influence of the unattended stimulus on a neuron's response. They hypothesized that the mechanism underlying this non-sensory response modulation was a change in the neurons' RF profile. Essentially, the neurons responded as if the RF had shifted towards and shrunk around the attended stimulus, effectively excluding the unattended stimulus from the RF (▣ **Fig. 1a**).

Other studies have demonstrated similar attentional modulation along the dorsal pathway. For example, Treue and Maunsell [23] used two oppositely moving dots within the RF of direction-selective neurons in area MT and showed that directing attention to one dot modulated the MT neuron's responses as if the influence of the second, unattended dot had been reduced. The same result was reported by Treue and Martinez-Trujillo [24] in 1999 using random dot patterns (RDPs). These and many findings in other areas of the visual cortex demonstrate that visual neurons are not invariant filters that exclusively encode their sensory input but that their response properties are modulated by the allocation of attention.

Feature-based attention as an additional influence

The studies mentioned above used behavioral tasks where spatial attention is shifted between stimuli inside the RF and the results are consistent with an attentional distortion of the RF. However, a different type of attentional modulation of neuronal responses observed after the initial studies on spatial attention provides an alternative interpretation.

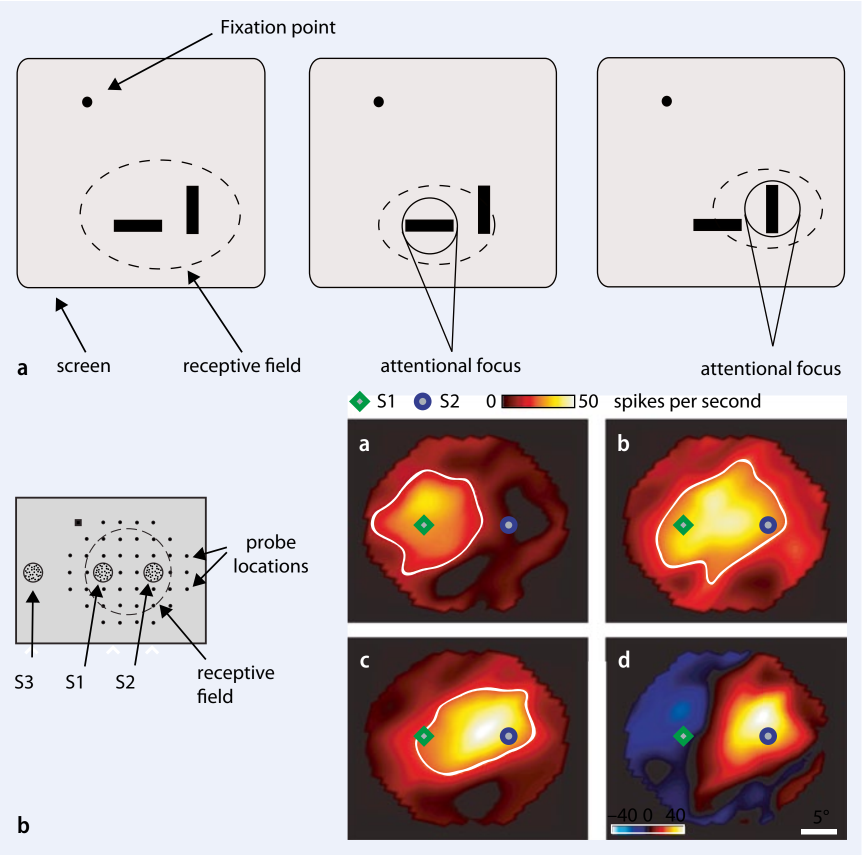

Fig. 1 ▲ Changes to receptive field profiles when focusing attention on one of several stimuli. **a**) Sketch of the experimental paradigm and presumed changes to the receptive field (*RF*) in the study of Desimone and Moran [14]. The dashed rectangle represents an example RF of a V4 neuron and the *blackbars* the stimuli (one at the preferred and one at a less preferred orientation). The *left panel* indicates the RF when attention is not directed into it. The *middle* and *right panels* indicate trials in which the animal was instructed to attend to one or the other stimulus and the presumed effect on the location and size of the RF. **b**) *Left panel* Sketch of the layout in the study of Womelsdorf et al. [25], depicting an example of the placement of the three moving random dot patterns (shown here as textured circles) that were present in every trial as well as the grid of locations at which a series of small probes could briefly appear within a trial. *Right panels* RF profiles of an example neuron, when attention was directed inside the RF, to stimulus S1 (**a**) or S2 (**c**), or when attention was directed outside the RF, to S3 (**b**). The surface color at each point in the plots indicates the increase in the neuron's response elicited by the presentation of a probe stimulus at that position, over the response observed in the absence of a probe (that is, when only S1 and S2 were present). **d** Difference map, computed by subtracting the RF when attention was on S1 from the RF when attention was on S2. The map illustrates that shifting attention from S1 to S2 enhances responsiveness around S2 and reduces it near S1. In this figure as well as in ◘ **Fig. 2 and** ◘ **fig. 3** the single dot represents the fixation point where the animal has to maintain his gaze throughout every trial

In a series of studies in area MT of the dorsal visual pathway Treue and Martinez-Trujillo [12] showed that attending to different motion directions outside of a neuron's RFs caused systematic changes in neuronal responses, even though spatial attention was far outside the RF. This phenomenon was called feature-based attention and led to the proposal of the feature-similarity gain model. It predicts the attentional modulation of visual neurons based on the similarity between a given visual neuron's preferences (RF location and tuning for non-spatial properties) and the attended stimulus' properties. When the animal's attention is well-matched to a given neuron's preferences the neuron's responsiveness is reduced, and when the attentional match is poor the neuron's firing rate is increased. This feature-based attentional modulation provided an alternative or additional account for the results observed when switching spatial attention between two stimuli inside a RF, as this always involved a switching between a preferred and a non-preferred stimulus. Thus, the attentional response modulation observed could reflect this change in feature similarity without a need to invoke a change in the receptive field profile.

To disentangle these two types of visual attention Treue and Patzwahl [18] used superimposed random dot patterns (RDPs) moving in opposite directions positioned inside the RF of MT neurons and instructed monkeys to attend to one of the RDPs and ignore the other. In this design, a shrinking of RFs could not account for the attentional modulation of responses since the two RDPs were fully superimposed and in the same fixation disparity plane, i.e., projected on the computer screen. They observed that the attentional modulation of responses was half of that observed when the RDPs were spatially separated inside the RF of the same neurons. This result pointed toward a combined effect of spatial attention (perhaps equivalent to a shrinking of the RF) and the feature-based attention effect observed by Treue and Martinez-Trujillo [24].

Directly measuring changes in receptive field profiles with attention

To directly determine whether the mechanism of spatial attentional modulation is indeed the reshaping of RFs, suggested by Moran and Desimone, it is necessary to map receptive fields while spatial attention is allocated to one or the other of two locations inside a given RF. This was the approach taken by Womelsdorf et al. [25]. They recorded the responses of single neurons in area MT of rhesus monkeys while the animals attended to one of two RDPs, moving in the same direction and positioned inside the recorded neuron's RF. The task for the animals was to sustain attention on one pattern while waiting for a change in its direction. By flashing probes at different locations inside and around the RF while the animal was waiting for the stimulus to change they could map a neuron's RF separately for each of the two spatial attention conditions. When the animal directed spatial attention to one of the patterns the RF shifted its center toward that attended stimulus' location. In addition, there was also a small shrinkage of the RF around that stimulus (▣ **Fig. 1b**). This systematic modulation of the spatial profile of the RF includes the antagonistic annulus that often surrounds MT receptive fields [2].

This finding provides a mechanism in support of the hypothesis that spatial attention can change a neuron's RF profile, such that the sensitivity of the attended region increases at the expense of the unattended parts. Thus, the original view outlined above of neurons in visual cortex as hard-wired, invariant filters for the location and other properties of visual stimuli has to be abandoned in favor of a system where neurons receive retinal input from a restricted region of the visual field but the sensitivity of different RF regions can dynamically change depending on the allocation of spatial attention.

Expansion of receptive fields during attentive tracking

The studies described above have focused on the role of spatial attention in producing a selective representation of behaviorally relevant stimuli. This function of attention is implemented by a reshaping of RFs in order to reduce the influence of irrelevant stimuli on neuronal responses. An additional important function of attention is to dynamically allocate processing resources to the relevant visual input. This flexible allocation is restricted across visual space towards attended locations and it is constrained by the RF boundaries. This is because the RF constrains a neuron's processing resources to input from a highly restricted region of space. Whether and to what extend the RF boundaries can be reshaped by attention has only recently been investigated at the level of single neurons. Niebergall et al. [17] trained macaque monkeys to attentively track two RDPs as they translated across a computer screen (▣ **Fig. 2a**) while recording from MT neurons. The motion paths of the tracked stimuli were designed to pass closely by or through a given neuron's RF. A comparison between neuronal responses to passing stimuli that were attended (tracked) or unattended (not tracked) revealed that in the former condition the RFs expanded toward the attended stimulus (▣ **Fig. 2b**). Interestingly, this effect was stronger at the RF boundaries, as if there was a selective increase of the neurons' RF sensitivity along those boundaries when facing the tracked stimuli. The consequence of such a systematic expansion of RFs is that the spatial path travelled by an attentively tracked stimulus is represented by more neurons than an untracked path. Thus, attentively tracking a moving object dynamically allocates additional processing resources to that stimulus representation.

Receptive fields when splitting the spotlight of attention

Insights from psychophysical and functional brain imaging studies suggest that the allocation of spatial attention is even more flexible and dynamic than addressed above. Some studies have shown that human subjects can simultaneously track multiple, independently moving objects without moving their gaze, i.e., they can split the 'spotlight' of spatial attention into more than one focus [4]. This ability is likely a major challenge for the systems that direct spatial attention internally but it is also an important adaptation to our complex environment that frequently contains more than one relevant stimulus or spatial location.

A recent study by Niebergall et al. [17], using single cell recordings in area MT of macaque monkeys provides evidence as to the potential neural correlate of the ability to split the focus of spatial attention during multi-object tracking. The observation that multiple moving objects can be tracked simultaneously is not by itself sufficient evidence for a split of spatial attention. Rather multiple object tracking might be achieved by simply enlarging the spatial attentional focus to enclose more than one stimulus. They therefore trained rhesus monkeys to track two RDPs that translated across a computer screen along parallel paths and passed a third RDP positioned inside a recorded neuron's RF (▣ **Fig. 3a**). This paradigm made it possible to record the response of MT neurons whose RFs fall between the two tracked objects. They tested the hypothesis that splitting the attentional spotlight across the two tracked stimuli would produce an area of suppression at the RF center, affecting the processing of the irrelevant RDP.

The changes in the RF profile of neurons in area MT were striking. When the two tracked patterns passed alongside or entered the RF the responses to the central stimulus in the receptive field was reduced, with the maximum suppression when the three patterns were aligned (▣ **Fig. 3b**). This result demonstrates that focusing spatial attention on the two translating patterns produced a suppressive area of inattention between them. This finding matches the observation reported by fMRI studies of spatially separated peaks of activity across the retinotopic spatial maps in the visual cortex when splitting spatial attention between two distant stationary stimuli [13, 15].

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Abstract

In the visual system receptive fields represent the spatial selectivity of neurons for a given set of visual inputs. Their invariance is thought to be caused by a hardwired input configuration, which ensures a stable 'labeled line' code for the spatial position of visual stimuli. On the other hand, changeable receptive fields can provide the visual system with flexibility for allocating processing resources in space. The allocation of spatial attention, often referred to as the spotlight of attention, is a behavioral equivalent of visual receptive fields. It dynamically modulates the spatial sensitivity to visual information as a function of the current attentional focus of the organism. Here we focus on the brain system for encoding visual motion information and review recent findings documenting interactions between spatial attention and receptive fields in the visual cortex of primates. Such interactions create a careful balance between the benefits of invariance with those derived from the attentional modulation of information processing according to the current behavioral goals.

Keywords

Attention · Vision · Rhesus monkeys · Cortex · Receptive field

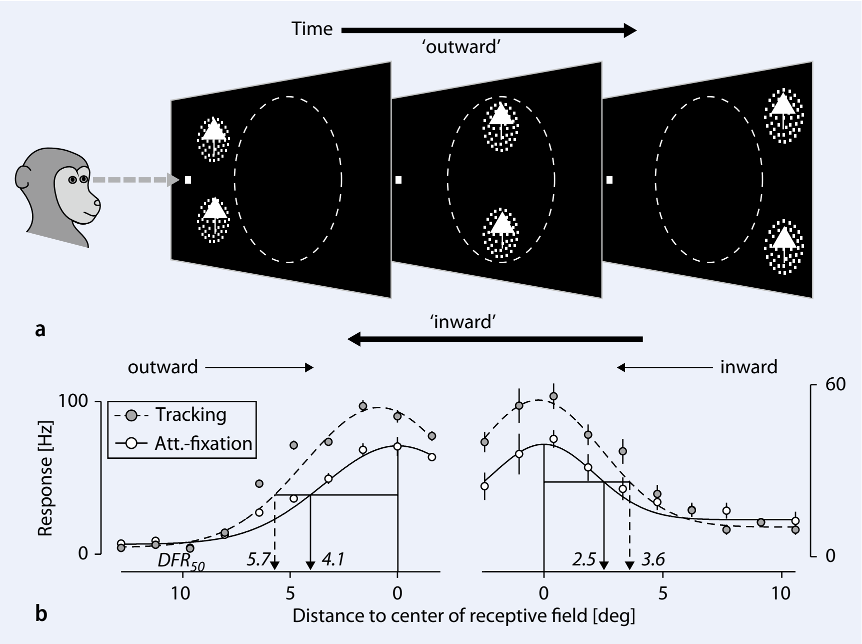

Fig. 2 ▲ Expanding receptive fields with attention. **a** Sketch of the experimental paradigm of Niebergall et al. [17]. Two random dot patterns (*RDPs*) moved across the screen following parallel trajectories (moving outward or inward relative to the fixation point) and moving through the peripheral parts of a neuron's receptive field (*RF*, *dashed circle*). During attend-fixation trials animals ignored the RDPs and had to detect a luminance reduction in the fixation point. During tracking trials animals had to detect a change in the local speed of the dots in one of the RDPs, which occurred at an unpredictable point in time. **b** Result from an example neuron. *Left panel* Data from 'outward' trials. *Right panel* Data from 'inward' trials. Data points represent the average responses evoked by RDPs with local dots moving in the neuron's preferred direction during tracking (*gray*), and attend-fixation (*white*). Gaussian fit predicted values are superimposed (*dashed line* tracking; *solid line* attend-fixation). The DFR$_{50}$ (*downward arrows*) represents the distance from the Gaussian center to the point of half-maximum response during attend-fixation (*horizontal line*)

A mechanism for changes in receptive field profiles with attention

The studies discussed above document a wide variety of attention-evoked changes in the structure of extrastriate neurons RFs: changes in the size and position as well as splitting RF profiles have been observed. While these changes are highly adaptive in a given attentional condition, it is unclear which mechanisms are responsible for such changes. An answer to this question might be provided by existing models of RFs in extrastriate visual cortical neurons. One of the most well-known RF models in extrastriate area MT was proposed by Simoncelli and Heeger [6, 22]. The model states that neurons in area MT receive excitatory tuned inputs from area V1 (linear integration step) and inhibitory input from neighbor neurons in area MT (normalization step). The latter is the sum of the total amount of activation in neighbor neurons, which is also determined by the inputs into the normalization pool. This model explains the sigmoid shape of the contrast response function of MT neurons, and it seems to be applicable to visual neurons in general [6]. How can we relate this model to the changes in the RF profiles observed in studies of attention?

Important clues come from studies that have examined the mechanisms of attentional modulation of responses to two stimuli inside the RF of extrastriate neurons. Ghose and Maunsell [5] recorded the responses of V4 neurons to two stimuli inside the units' RF. They also recorded the responses to each one of the stimuli alone. Then they tried to reconstruct the responses to the stimulus pairs from the responses to the single stimuli using an input summation model. By modulating the individual inputs into V4 neurons they could account for the attentional modulation of responses to two stimuli and reconcile apparently contradictory observations made by previous single cell studies of attention.

Another input model of attention was proposed by Reynolds and Heeger [19]. In their approach, attention also modulates responses of extrastriate neurons in a given area by modulating inputs into neurons. This modulation affects the intensity of the normalization mechanism that causes response saturation [1]. This input-normalization model also explains the effect of attention on the contrast response function of extrastriate visual neurons [11, 20]. As an alternative to these input models, Lee and Maunsell [10] proposed that attention may act by controlling the intensity of the normalization step (i.e., the firing rate of neurons in the normalization pool). It should be pointed out that despite differences in details these models are very similar and provide good accounts for most of the known modulatory effects of visual attention.

Evidence in favor of changes in the strength of input signals into extrastriate visual neurons with attention has been provided by Khayat et al. [8]. They recorded the responses of MT neurons from two macaque monkeys to two stimuli inside their RF while varying the contrast and direction of one of the stimuli. By instructing the animals to switch attention between different stimuli they observed a modulation of the neurons' firing rate that was incompatible with a modulation of responses at the level of MT neurons by a gain control mechanism. The results were better explained by a modulation of inputs into MT neurons. Moreover, in a related study the same authors demonstrated a modulation of local field potentials (LFPs) recorded in area MT compatible with a modulation of inputs into the area. They proposed that a modulation of responses of V1 neurons feeding into MT [3], which contribute the most to the LFPs high frequencies [9], would account for the observed pattern of modulation.

The proposed mechanism of changes in the RF profile with attention is illustrated in ◘ **Fig. 4**. Here a layer of neurons with small RFs (e.g., V1 neurons) feeds into an MT neuron. The connectivity strength of each neuron is determined by the weight function that approximates a Gaussian shape [21]. The contribution of neurons in the middle is larger than the one of neurons at both sides; thus, the MT RF also approximates a Gaussian function but it is much larger than the input neurons' RFs. Note that although this is illustrated in one dimension this applies in the same way to a two-dimensional model of the RF. The effects of attention can be simulated by applying different gains to different neurons in the input layer (◘ **Fig. 4b**; [26]). In this case by increasing the contribution of neurons on the right and decreasing the one of neurons on the left side one can obtain a shift of the RF to the right. Different transformations are possible by using different patterns of modulation (e.g., multiply the weight function by differently shaped functions that describe how attention acts on the input layer). Note that in this simplified model we have not considered the normalization step (i.e., inhibition of an MT neuron by its neighbors). However, it is also possible that a modulation of the normalization pool activity contributes to changing the shape of RFs, e.g., to the non-linear changes observed by Niebergall et al. [16, 17] during tracking. Building a quantitative model that captures the dynamics proposed in ◘ **Fig. 4** and that generates testable new predictions remains a challenge for future studies of attention.

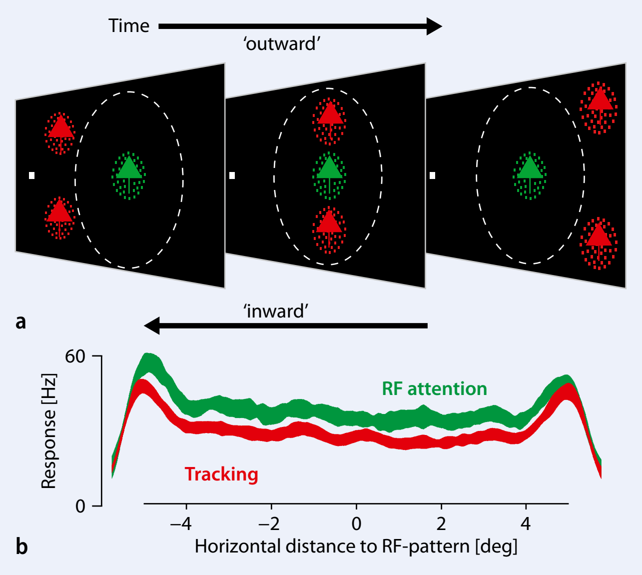

Fig. 3 ▲ Splitting receptive fields with attention. **a** Sketch of the experimental paradigm of Niebergall et al. [17]. The experiment was identical to the one described in ◘ **Fig. 2**, except that a third RDP (with local dot motion in the neuron's preferred direction) was placed and stayed in the center of the RF and that the animal was instructed to attend either to the translating RDPs (*tracking*) or to the RF stimulus (*RF attention*). **b** Response modulation between *tracking* and *attend RF*. Data from an example cell for the stimulus configuration with the translating RDPs dots locally moving in the preferred direction. The plot shows average responses (± SEM) as a function of the translating RDPs' position during attend RF (*green*) and tracking (*red*) trials

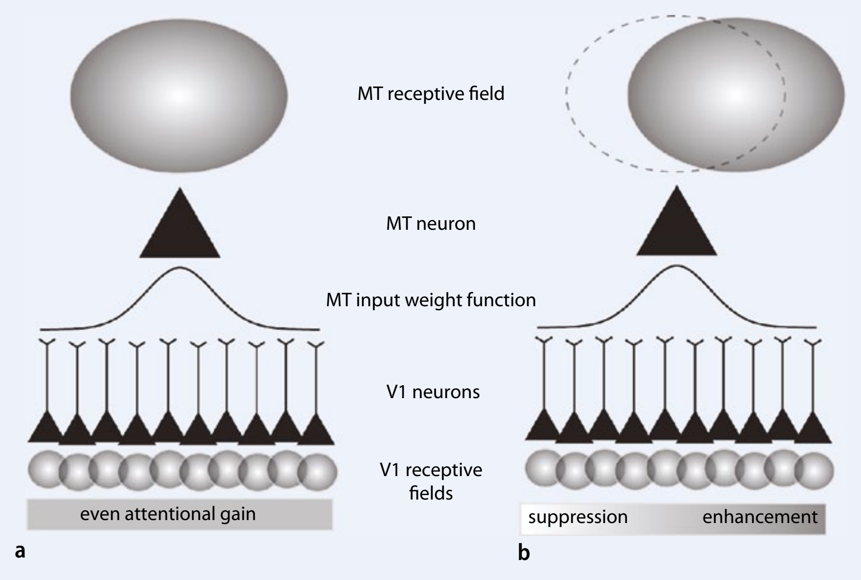

Fig. 4 ▲ A possible mechanism for the attentional shift of receptive fields. The two panels are sketches of the putative V1 inputs into an MT neuron. The small circles at the bottom indicate the RFs of the V1 input neurons along a horizontal axis crossing the middle of the MT receptive field. Each *small triangle* represents the cell body of a V1 neuron and the connected lines the projection toward the MT neuron (*large triangle*). The *bell-shaped function* represents the strength of the weights from the V1 neurons into MT. **a** The *large ellipse* represents the MT neuron's RF. The *gray band* at the bottom represents the even attentional gain applied to all V1 neurons in the absence of a spatial focus of attention. **b** If attention is directed to the right, the attentional gain increases for the right V1 neurons and decreases for the left V1 neurons. This causes the MT RF profile to shift towards the right. The *dashed ellipse* represents the old RF and the *filled ellipse* the new RF in the presence of spatial attention on the right side

Conclusion

Investigations of the detailed effects of spatial attention on the response properties of individual neurons in primate visual cortex have revealed a great deal of flexibility in the profile of receptive fields (RF). Contrary to the classical view of RFs as static hard-wired entities that form the central component of encoding the incoming sensory information it is now apparent that RFs are a highly flexible component in the attentional system. By being able to dynamically alter its RF properties the visual system is able to fulfill two core goals of attentional modulation of information processing, namely the suppression of irrelevant information and the allocation of additional resources to the processing of relevant incoming sensory information. Given the

importance of a balance between the benefits and disadvantages of a stable system (simplifying information processing) and a highly adaptive and dynamic system, evolution seems to have opted for a compromise. The changes to RFs imposed by attention stay within a well-circumscribed range while still adapting to the attentional demands of a given situation, in essence combining the benefits of a stable and a dynamic system.

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