

Neural correlates of attention in primate visual cortex

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The processing of visual information combines bottom-up sensory aspects with top-down influences, most notably attentional processes. Attentional influences have now been demonstrated throughout visual cortex, and their influence on the processing of visual information is profound. Neuronal responses to attended locations or stimulus features are enhanced, whereas those from unattended locations or features are suppressed. This influence of attention increases as one ascends the hierarchy of visual areas in primate cortex, ultimately resulting in a neural representation of the visual world that is dominated by the behavioral relevance of the information, rather than designed to provide an accurate and complete description of it. This realization has led to a rethinking of the role of areas that have previously been considered to be 'purely sensory'.

The senses of humans and other highly evolved animals are an evolutionary success story. In the visual system of primates, as many as 1.5 million axons exit the retina, supplying a wealth of detailed information about the visual environment. Yet at any given moment, much of this information is behaviorally irrelevant. If evolution had not also endowed the nervous system with mechanisms to control the flow of information, only a small fraction of our processing capabilities could be devoted to crucial aspects of the incoming sensory signals. The development of a fovea, combined with the ability to make fast and accurate eye movements are among the sensory specializations that are aimed at sifting the wheat from the chaff in visual information processing. In addition to these bottom-up mechanisms, the visual system uses attention as a powerful top-down influence to optimize the use of its processing resources, by allowing us to concentrate processing on a very small proportion of the incoming information. We do experience the allocation of attention as effortful, but the extent to which it restricts processing seems to escape intuition, as demonstrated by our inability to detect even large changes in visual scenes as long as they occur outside the focus of attention¹.

This article gives an overview of neurophysiological studies of top-down attentional influences that have used single cell recording techniques in the visual cortex of behaving monkeys. (For a discussion of recent developments in the psychophysics of attention, of brain imaging approaches and of attentional influences, particularly in parietal cortex, see Refs 2–5.)

Investigations of the neural correlates of attention need to demonstrate that changing attentional conditions will change neuronal responses in the

absence of sensory changes. The effects observed need to show the two characteristic features of attention that have been established in psychophysical studies: (1) attention changes how sensory information is processed; and (2) this modulation is selective, i.e. not all sensory signals are equally affected. These two central aspects of attention provide us with a framework for outlining some of the advances in our understanding of attentional influences on visual information processing.

Selectivity

The results of early studies suggested three conclusions on the neural basis of attentional selectivity: (1) attentional influences seemed to be restricted to higher areas of extrastriate visual cortex; (2) responses would be modulated when the 'spotlight of attention' was directed into (versus out of) the receptive field of a neuron, i.e. the area of the visual field from which the neuron can be activated; and (3) directing attention into the receptive field would enhance the responses of the neuron.

Each one of these three conclusions has had to be substantially refined or revised in light of more recent findings.

Attentional modulation in early extrastriate and striate cortex

The ease and reliability with which strong attentional influences could be demonstrated in higher extrastriate cortex, the apparent gradient in the strength of attentional modulation along areas of the ventral cortical pathway and the failure of several studies to find clear attentional effects in primary visual cortex^{6,7} has led to the view that visual cortical processing starts with a purely sensory analysis of the incoming information in area V1. This information is then passed on to the two main processing streams for visual information, the ventral pathway [which passes through areas V2 and V4 into inferior temporal visual cortex] and the dorsal pathway [which passes through the middle-temporal area (MT) and the medial superior temporal area (MST) into the parietal cortex]. In the ventral pathway, attentional effects could be demonstrated early in the hierarchy, but they seemed to be restricted to tasks in which two stimuli were presented in the same receptive field⁸. The dorsal pathway seemed to maintain its purely sensory characteristics longer, with reports that the earliest

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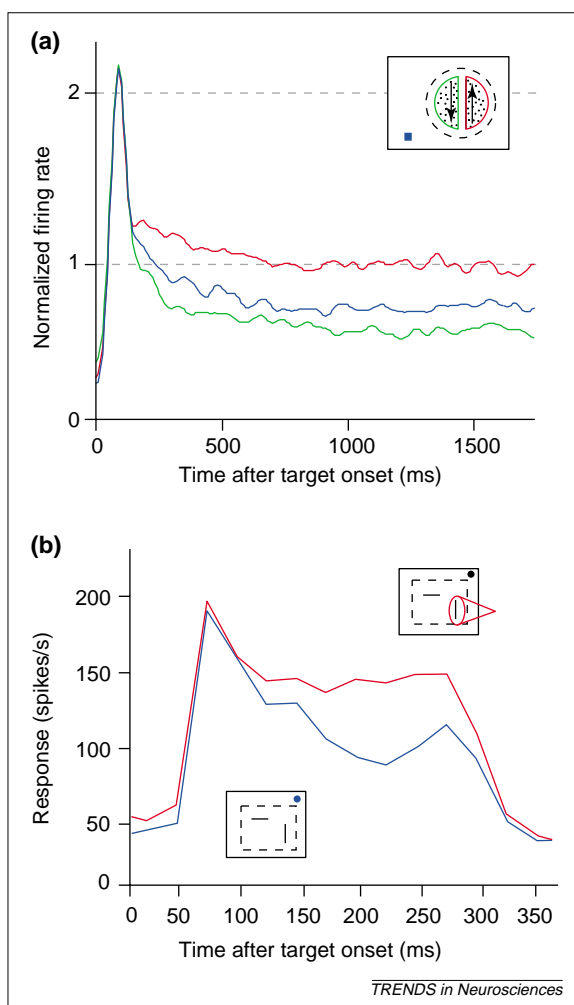


Fig. 1. Time course of responses to two stimuli inside the receptive field. (a) The curves indicate the normalized instantaneous firing rate averaged across 64 cells from the middle-temporal area (MT) and the medial superior temporal area (MST). The x-axis plots the time (in ms) from the onset of the stimuli. The y-axis is the level of response relative to the sustained activity in the condition where attention was directed towards the preferred direction stimulus inside the receptive field. The inset is a cartoon of the stimulus conditions. Two half-circle shaped random dot patterns were presented inside the receptive field, one moving in the preferred direction and the other in the anti-preferred direction of the neuron. The animal was instructed before every trial to direct its attention towards one or the other pattern (red and green curve), or to a square on top of the fixation cross (blue curve). (b) The two curves plot the firing rate of a V2 cell. Two oriented bars were presented inside the receptive field for 200 ms. The upper curve is the response when attention was directed towards the bar with the preferred orientation and the lower curve plots responses in the 'neutral' condition, when attention was directed outside the receptive field. Note that in both cases attentional modulation sets in later than the sensory response. This could be caused by response saturation in the onset response or could be a reflection of a genuine delay between the two effects. (b) Modified, with permission, from Ref. 37.

systematic extra-retinal influences appeared in area MST (Refs 9–11).

But the view that V1 performs a purely sensory analysis of the incoming information and of the difference between attentional effects in the two pathways had to be abandoned in light of studies in the 1990s. First, electrophysiological^{12–15} and

imaging^{16–20} studies were able to demonstrate convincingly that visual information processing in V1 is influenced by the attentional conditions (see Ref. 21 for a review). Second, PET imaging experiments^{22,23} and a study²⁴ in an individual suffering from a bilateral lesion of the human MT homolog showed specific attentional influences in early areas of the human dorsal visual pathway. These studies were followed by electrophysiological experiments that demonstrated attentional modulation of visual motion processing in area MT of macaque cortex^{25–30} and by functional magnetic resonance imaging studies that showed similar effects in the presumed human homolog^{31–33}. By now, imaging studies had traced these attentional effects on motion processing all the way back to V1 (Refs 34,35). Taken together, these studies demonstrate that attention influences processing in both pathways from the beginning, but they also indicate that the magnitude of attentional modulation increases as one moves up the cortical hierarchy. The neural signals mediating these top-down modulations presumably use the extensive feedback projections from higher to lower areas present throughout visual cortex.

The combination of early modulation with a graded increase in higher areas combines aspects of the two theories of attentional selection that dominate the psychophysical literature: the early and late-selection theories. The visual system seems to perform some early selection of inputs with further selection in areas that contain more complex representations of the visual environment. However, electrophysiological studies provide no apparent support for the dichotomy, which is advanced in the psychophysical literature on visual search, between visual features that can be processed pre-attentively and those that cannot, because the processing of all visual features seems to be susceptible to attentional influences.

Response modulation when directing attention into versus out of the receptive field

Attention has often been likened to a spotlight, suggesting as a neural correlate an enhanced response of a sensory cell when spatial attention is switched from outside into the receptive field. While some reports from the ventral pathway report difficulties generating reliable and systematic modulations using such a paradigm^{7,8,12}, other studies and studies in the dorsal pathway report modulated responses when attention is directed into the receptive field of neurons from almost every area in visual cortex tested^{12,25,26,36,37}. The findings that stimulus contrast³⁸ and task difficulty³⁹ influence the magnitude of attentional modulation provide possible explanations for these differences.

The data suggest an attentional system that activates cells with receptive fields that overlap the 'spotlight of attention'. But an attentional system that

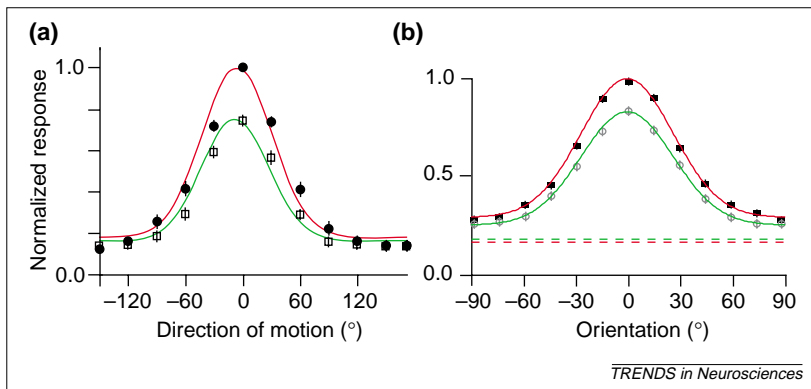


Fig. 2. Average tuning curves to an attended and an unattended single stimulus inside the receptive field. The upper red curve in both plots represents the response when attention was directed towards the stimulus inside the receptive field, whereas the lower green curve is the response to the same stimulus when attention was directed out of the receptive field. In both curves the attentional modulation did not change the tuning width significantly. (a) Average tuning curve across 35 cells from the medial superior temporal area (MST) to the direction of a high contrast moving random dot pattern. (b) Average tuning curve across 197 V4 cells to the orientation of a grating. The broken lines represent the respective background firing rates, i.e. the responses of the cells in the absence of a stimulus. Note that background firing rates along the temporal pathway tend to be higher than in the dorsal pathway. This effect is even more pronounced here, presumably because of the lower dynamic range of response caused by the lower contrast stimuli used. (b) Modified, with permission, from Ref. 36.

would be able only to modulate responses depending on the presence of the 'attentional spotlight' inside versus outside the receptive field would have very poor spatial resolution beyond striate cortex and the few other cortical areas with small receptive fields. Instead, our visual system seems able to precisely allocate attention, even in the presence of nearby unattended stimuli.

Differential attentional effects inside the receptive field

To address this issue, several studies^{7,26,28,29,37,40} have trained monkeys to direct their attention to one of two stimuli inside the receptive field, an approach pioneered by Moran and Desimone⁸. One stimulus was matched to the sensory preferences of a cell, whereas the other was not. Responses are generally substantially higher in trials where the animals were attending to the preferred stimulus (Fig. 1), demonstrating that attentional modulation has a better spatial resolution than the size of the receptive fields. This allows attention to overcome the apparent limit to its spatial resolution imposed by the large receptive fields in higher areas of visual cortex.

Attention can suppress responses

The response modulations that are demonstrated when switching attention from outside to inside the receptive field suggest that directing attention into the receptive field always enhances responses. To investigate this conjecture, a 'neutral' or 'sensory' condition can be used where attention is directed outside the receptive field, i.e. when both stimuli inside the receptive field are behaviorally irrelevant^{7,29,37}. When directing attention towards the preferred stimulus inside the receptive field, the

response of the neuron is increased, but the response of the neuron will often drop below the neutral response when attention is directed to the other stimulus. Switching attention between two stimuli inside the receptive field combines the suppressive effect of attending to the non-preferred stimulus with the enhancing effect of attending to the preferred stimulus. This push-pull interaction might be one of the reasons that the attentional modulation is stronger in experimental paradigms that juxtapose two stimuli inside the receptive field.

These findings suggest that attention does not unspecifically increase the responsiveness of a neuron but rather can specifically enhance the influence of the attended stimulus at the expense of unattended stimuli, or modulate the overall responsiveness of a neuron based on the relationship between its preferred stimulus features and the currently attended stimulus features and spatial location. These two alternate interpretations are at the core of two models (the biased competition model⁴¹ and the feature similarity gain model²⁹), which try to account for the influence of attention on neuronal responses.

Non-spatial attentional modulation

The spotlight metaphor suggests a special role for spatial location as the basis for attentional selection, but several studies have demonstrated non-spatial, feature-based attentional modulation as well. Chelazzi and colleagues have demonstrated increased responses in inferior temporal cortex, even before the onset of the preferred shape of a neuron, if its appearance was expected and behaviorally relevant^{40,42}. Motter trained monkeys to discriminate the orientation of a bar that matched the color of a cue and found enhanced responses in V4 when the bar in the receptive field was of the cued color^{43,44}.

Recently, feature-based attentional modulation that reaches far beyond the confines of the spatial receptive field of a sensory cell has been reported in the dorsal pathway²⁹. The activity of MT neurons is larger when the animal is attending to a preferred-direction stimulus versus an anti-preferred one, even when the attended stimulus is far from the receptive field. Attending to a particular feature, such as a direction of motion, thus seems to enhance the responsiveness of all neurons that prefer this stimulus feature, not just of those whose receptive field includes the attended stimulus. This feature-based attentional modulation is of comparable strength with spatial attentional modulation, and the two influences combine additively in appropriate experimental paradigms, properties that are also observed in the ventral pathway⁴⁵.

These findings of non-spatial attentional modulation are well matched by a number of functional brain imaging studies that have also

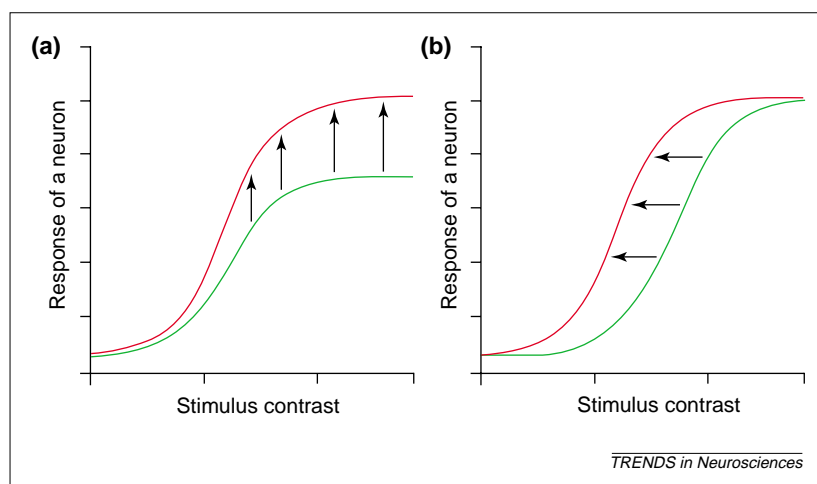


Fig. 3. Hypothetical effects of attention on the contrast response function. The x-axis plots stimulus contrast and the y-axis the response of a neuron. The green and red curves depict the responses to an unattended and attended stimulus, respectively. (a) Multiplicative change of the contrast response function. Note that the attentional effect, expressed as the proportional change in firing rate, is constant across the curve. (b) Effect of a change in apparent contrast by attention. If directing attention to a preferred stimulus were to increase this stimulus' effective contrast, it would shift the contrast response function leftwards. Such a modulation would create large changes in response at intermediate levels of contrast, whereas at low and high contrast levels, attentional modulation would be small.

reported modulations in the absence of shifts of the spatial location of attention^{20,22,23,31–34,46}, but even a combination of spatial and feature-based attentional effects cannot account for all attentional phenomena observed physiologically, such as the object-based attentional modulation observed in V1 (Ref. 13) and the specific attentional effects on the modulatory influence of the visual context surrounding an attended stimulus¹⁴.

Modulation

The modulations in firing rate caused by the attentional selection processes discussed above can be very strong. But the prime modulatory influence is the sensory stimulus itself (although attentional modulation has also been reported in the absence of sensory stimulation^{7,47}). Comparing attentional modulation with the much better understood sensory modulation might offer important insights into the mechanisms of attentional influence. This has been addressed in two ways: attentional modulation of tuning curves and direct comparisons between the effects of stimulus contrast and attention.

Attentional modulation of tuning curves

Spitzer and colleagues were the first to investigate how attentional modulation changes sensory selectivity³⁹, i.e. the tuning curve of a neuron, which plots the response of a neuron as a function of a continuous stimulus property such as orientation. They have compared tuning curves in area V4 during easy and difficult discrimination tasks, i.e. when the monkeys were presumably paying less (easy task) and more (difficult task) attention to the stimulus. They report that orientation and color tuning curves

were narrower when the task was more difficult, suggesting that the selectivity of the cells was changed by attentional modulation.

Recently, McAdams and Maunsell have addressed the issue again with a paradigm in which attention was either directed onto the orientation of a sine-wave grating inside or the color of a second grating outside the receptive field³⁶. By changing the orientation of the gratings, they were able to determine orientation tuning curves for V1 and V4 cells to an attended and unattended stimulus (Fig. 2). The observed attentional modulation was a purely multiplicative one, i.e. the two tuning curves did not differ in their tuning width but only in their respective heights, a behavior also reported for direction tuning in the MT and MST (Ref. 29). McAdams and Maunsell also demonstrated that attention left response variability (the relationship between neural response rate and the variance) unchanged⁴⁸. Several differences between the Spitzer and McAdams studies, which include stimulus conditions, task demands and data analysis, have been suggested as the basis of the discrepancy.

The issue of whether attention is able to change the tuning behavior of cells in visual cortex is of particular importance, as the presence or absence of such effects would provide important constraints for models of the mechanisms of attentional modulation^{49,50}.

Spatial tuning as a special case?

Although the data discussed above suggest very similar multiplicative attentional operations across visual pathways and encoded stimulus features, one notable exception does seem to exist. Connor *et al.* have reported shifts in receptive field centers in V4 towards an attended location^{51,52}. These effects are very reminiscent of the suggestion, originally advanced by Moran and Desimone⁸, that spatial attention might contract a receptive field around an attended location. While such changes in spatial tuning curves cannot be achieved directly through a multiplicative modulation, Maunsell and McAdams⁵³ have argued that they can be accounted for by an appropriate multiplicative modulation of the input neurons in the preceding cortical areas. Spatial tuning might be a special case because it is the only domain where substantial changes in tuning width occur as one progresses through the hierarchy of visual cortical areas. A multiplicative change in one area can therefore lead to non-multiplicative effects in later areas. It remains to be seen if such effects can also be observed in other, more complex tuning properties in sensory cortex.

Comparing response modulation by contrast and by attention

The multiplicative attentional modulation based on the behavioral relevance of stimuli is very

reminiscent of the modulatory influence of stimulus parameters, such as contrast⁵⁴, speed⁵⁵ and motion coherence⁵⁶, on sensory responses. This similarity suggests a shared neural mechanism in which attention changes the strength of a stimulus by changing its 'effective contrast' or saliency, but it might simply reflect two independent multiplicative systems.

It is difficult to prove such a shared mechanism, but one of its predictions is that a non-linearity in sensory coding should also create non-linearities in the attentional modulation. Such a sensory non-linearity is the sigmoidal shape of the contrast response function of most sensory cells (Fig. 3). If the multiplicative effect of attention should influence the firing of a cell independently of the encoding of stimulus contrast, the contrast response function should be stretched vertically in the same way as the tuning curves in Fig. 2, creating an attentional modulation that is independent of stimulus contrast (Fig. 3a). If, alternatively, attention changes the effective stimulus contrast, in effect shifting the contrast response function horizontally, response modulations should be stronger for stimuli of intermediate luminance or contrast (Fig. 3b).

Reynolds and his colleagues have observed just such an effect in area V4 (Refs 38,57). Similarly, studies in the MT and MST have demonstrated attentional effects (as percentage changes in response levels) that are stronger when the luminance of the stimuli lay along the steep part of the contrast response function of the cell^{58,59}. Reynolds *et al.* have argued that this dependency of the magnitude of attentional modulation might account for the differences in attentional modulation observed between studies that have used different contrast levels. Although these experiments are in agreement with the intriguing idea that sensory and attentional influences might share neural mechanisms, alternative explanations for the similarity of sensory and attentional modulation need to be ruled out before the neurophysiological findings can provide an account for the influence of attention on stimulus saliency observed in higher cortical areas⁶⁰ and in psychophysical studies^{61,62}.

Concluding remarks

In summary, our understanding of attentional modulation of sensory responses has come a long way. Recording studies in awake behaving monkeys have demonstrated attentional modulation for most areas

Unanswered questions

- Can a careful analysis of the time course of attentional modulation, both within and across areas, help in determining the mechanisms and the source of attentional signals?
- Models have been proposed that suggest or even require tuning curve sharpening by attention: how can the apparent discrepancy with the observed multiplicative attentional modulation be resolved?
- If the systems for encoding stimulus properties and the behavioral relevance of the stimuli are closely intertwined, does this mean that conditions exist in which effects of changes in stimulus contrast and the allocation of attention cannot be perceptually distinguished?
- Is the change in response caused by attention in early visual cortical areas large enough to account for psychophysical effects of attention, or are other areas needed that might show stronger attentional effects and possibly include non-multiplicative changes of stimulus selectivity?

of visual cortex, starting in primary visual cortex and increasing in magnitude in extrastriate areas. Attentional modulation can be observed with single stimuli inside the receptive field of a neuron, but is stronger when the enhancement of attended and the suppression of the unattended stimuli are combined in a push-pull fashion, i.e. when both are within the same receptive fields. Attentional modulation is not restricted to the spatial domain. Rather, attention to other stimulus features, such as the direction of motion, recruits cells whose preferred features are similar to the features of the attended stimulus. The modulation itself seems to be multiplicative, preserving the shape of the tuning curves of the neuron. The similarity and interaction between the multiplicative modulation exerted by of the top-down influence of attention and by the bottom-up influence of stimulus contrast makes the intriguing suggestion that these two mechanisms share common neural mechanisms. Many questions remain unanswered, but the multitude of techniques (including single cell recordings, psychophysics, functional brain imaging, electroencephalography and magnetoencephalography) that can now be applied and combined suggest that the enormous rate of progress in the past few years can be maintained.

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