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Visual attention: the where, what, how and why of saliency

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Attention influences the processing of visual information even in the earliest areas of primate visual cortex. There is converging evidence that the interaction of bottom-up sensory information and top-down attentional influences creates an integrated saliency map, that is, a topographic representation of relative stimulus strength and behavioral relevance across visual space. This map appears to be distributed across areas of the visual cortex, and is closely linked to the oculomotor system that controls eye movements and orients the gaze to locations in the visual scene characterized by a high salience.

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Abbreviations

FEF frontal eye field
fMRI functional magnetic resonance imaging
LGN lateral geniculate nucleus
MT middle temporal area

Introduction

Through most of our waking life our eyes (as well as our other senses) provide us with a barrage of signals about our environment. Usually we can (and want to) process only a miniscule amount of this stream of information with the chosen few bits and bytes usually being the ones that reach our awareness, and the ones able to go into our memory [1].

The selection process that underlies the decision of which of the information that is entering our eyes receives further processing therefore plays a central role in sensation, serving as the gatekeeper that controls access to our highly evolved visual information processing system. This process reflects bottom-up aspects, that is, properties of the incoming sensory signals, as well as top-down influences that represent the internal state of the organism. A less unified system has been proposed by Corbetta and Shulman [2] that suggests that there is a partial segregation of the bottom-up and the top-down process into two interacting networks of brain areas.

Here, I review evidence that suggests that primate visual cortex is the implementation of a multi-stage selection process, in which bottom-up stimulus features and top-down attentional modulation are combined such that relevant information is continuously favored, emphasized and ultimately analyzed at the expense of information deemed to have lesser relevance. This process combines sensory information and attentional modulation to create an integrated saliency map of the visual environment that flags regions of interest in the retinal image, and can serve to guide gaze shifts to these locations. This saliency map is created through hardwired properties, such as the opponent center-surround organization of many visual neurons, as well as by dynamic influences, such as attention. The resulting sparse representation of the visual environment reflects the system's best guess as to the most relevant information. The reliance on the most salient aspects might not always be appropriate but it is an effective use of limited processing resources, as aspects of low salience require more processing because of their poor signal-to-noise ratios.

At the front end of the system, that is, the retina, the selection process appears to be formed entirely on the basis of bottom-up stimulus aspects. Most notably, the pixel-by-pixel representation of the visual environment created by the photoreceptor matrix is compressed into a representation emphasizing discontinuities. This process starts with the opponent center-surround organization of the receptive field of the retinal ganglion cells that makes them particularly responsive to edges in the luminance profile while preventing a response to homogeneous illuminations. This process continues with neurons in the visual cortex that show a similar suppressive center-surround organization for stimulus aspects, such as orientation and direction of motion.

Where: locating attention

Although the first reports of attentional modulation of sensory signals in extrastriate cortex appeared about two decades ago [3–6], one focus of recent efforts has been to unambiguously establish such influences in the early stages of the visual processing hierarchy. There are now several electrophysiological [7–11] and a large number of functional imaging [12–22] studies that demonstrate attentional influences in primary visual cortex, V1. Correspondingly, practically all cortical visual information processing is shaped by top-down attentional influences; a purely sensory representation of the visual environment does not appear to exist in primate visual cortex. A recent functional magnetic resonance imaging (fMRI) study by O'Connor and colleagues [23•] has brought top-down

influences even closer to the retina by reporting attentional modulation of activity in the lateral geniculate nucleus (LGN) of the thalamus. They report enhanced baseline activity in the LGN without a stimulus when subjects were expecting the appearance of a stimulus. Furthermore, they find increased activity to attended versus unattended flickering checkerboard patterns, as well as reduced responses to those stimuli when attention was engaged in a different task.

Although attention seems to influence almost all of the visual cortex, its modulatory power follows a clear gradient. As one moves up the cortical processing hierarchy, the strength of attentional effects dramatically increases [24[•]]. While attentional effects amount to only a few percent in early visual cortex, unattended stimuli are almost completely suppressed in prefrontal [25] and parietal cortex [26], with lesions in the parietal cortex severely impairing the ability to filter out irrelevant information [27].

It is unclear if the representation in areas of the frontal cortex should be considered to be the basis of perception, with the activity patterns in visual cortex feeding into this final representation without directly influencing perception or performance. Alternatively, the multiple representations in visual and frontal cortex could represent a distributed saliency map, in which perception would be based on the activity in the area whose neuronal properties are best matched to the current perceptual task. In favor of the latter hypothesis is the finding by Cook and Maunsell [24[•]] that during a task in which monkeys had to detect the appearance of a coherent motion signal the average neuronal performance in VIP, the highest area they recorded from, exceeded the average behavioral performance of the animal, whereas in the middle temporal (MT) area, which represents an earlier level of processing, the inverse was found. This suggests that an intermediate area, such as the middle superior temporal area (MST), might provide the best correspondence between neuronal and behavioral performance for their task.

What: places, faces, features and objects

It is important to understand what is selected by attention. Traditionally, attention research, particularly electrophysiological studies in primate visual cortex, has focused on spatial attention, a selection based on the location of a stimulus. The popular spotlight metaphor captures the essence of spatial attention by comparing it to a flashlight that illuminates a region of interest, which thus allows for increased sensitivity and a more precise encoding of information from this spatial location. Recordings from single cells in areas along the two processing pathways of the visual cortex in awake rhesus monkeys that are trained to perform attentional tasks have demonstrated the neural basis of such spatial selec-

tion. Directing attention into the receptive field of these neurons will often modulate the cell's firing rate, resulting in an increased or decreased activity. Specifically, directing attention to a stimulus matching the cell's preference will tend to increase responses, whereas drawing attention to an unpreferred stimulus usually results in a lowering of the number of responses (see Treue and Assad [28,29] for reviews).

More recently, electrophysiological studies have investigated feature-based, non-spatial attentional effects [30,31]. They demonstrate that directing attention to a cell's preferred feature even as far outside its receptive field as the opposite hemifield will enhance a cell's responsiveness or gain. However, switching attention to the cell's non-preferred feature at the same distant spatial location will decrease firing rates when compared to a neutral condition in which the animal performs an attentional task unrelated to the cell's sensory preferences. This global feature-based attentional modulation has recently been confirmed to also occur in the human MT-complex [32]. Changes in the attended feature have been a part in almost all early physiological experiments involving shifts in spatial attention, and are likely to contribute to the response suppression that is reported when attention is switched to a non-preferred stimulus inside the receptive field. It has been difficult to distinguish feature-based attention from object-based attention physiologically, with the notable exception of a series of experiments in primary visual cortex involving a task in which the animal was trained to mentally trace a curved line, resulting in enhanced activity of neurons whose receptive field is intersected by this line. Investigations of object-based attention have played a more prominent role in fMRI studies of higher visual areas selectively responsive to such objects as faces or houses [33]. Here, the allocation of attention to such objects activates the corresponding area as well as areas coding the motion of the attended object. This fulfills the criterion for distinguishing feature-based attention from object-based attention, namely the spread of attentional enhancement to unattended features of attended objects. Similarly, psychophysical studies have provided strong evidence for an attentional system that is not restricted to the spatial location or to any other single stimulus feature, but rather spreads across multiple dimensions of the same object or surface [34,35]. Physiological examinations of these phenomena will help to bridge the traditional gap between investigations of feature-based effect in physiology and object-based accounts for psychophysical performance.

How: merging bottom-up and top-down saliency

The attentional modulations of neural activity in visual cortex outlined above all result in an enhancement of the activity or the synchrony [36[•],37] of cell populations that prefer attended stimulus attributes, and a simultaneous

suppression in the activity of cell populations that prefer non-attended attributes. This will create an enhanced representation of attended relative to unattended stimuli, an effect reminiscent of the selective enhancement of particular aspects of the visual input by the hardwired bottom-up coding mechanisms mentioned above. The similarity of the two systems suggests their integration into a common saliency map, in which the visual input is represented not by the physical strength of an individual stimulus (such as its luminance) but by its saliency, that is, its difference in properties compared to the surrounding visual input. This bottom-up saliency is then combined with the modulatory influence of attention, strengthening or weakening the bottom-up saliency on the basis of the behavioral relevance of a particular location, feature or object. Two recent studies [38,39,40] have directly investigated the interaction between contrast, the most general saliency factor, and attention in the ventral and dorsal visual pathway. Both studies demonstrate that attentional modulation effectively enhances stimulus contrast. Because of the s-shaped contrast response function of visual neurons, this leads to the largest attentional changes in neuronal responses for stimulus luminances causing intermediate neuronal responses rather than simply providing a constant response modulation across all stimulus strengths. This interaction points to a central function of attention in enhancing the representation of stimuli of intermediate strength, whereas particularly salient stimuli will be well represented even in the absence of attention. This theory is in good agreement with a large body of psychophysical studies (for example see Nothdurft [41]) that demonstrate that highly salient stimuli (known as 'pop-out' stimuli in visual search tasks) need little attentional resource allocation, whereas the same stimuli embedded amongst similar distractors will only be perceived when attention is directed towards them.

Why: putting it all to good use

For simple psychophysical tasks the existence of a strong corresponding stimulus representation in the saliency map might be sufficient [42,43], but more demanding visual tasks will require the high-resolution scrutiny that can only be provided by the fovea. This will generally require a gaze shift, and a saliency map represents potential targets for upcoming eye movements that can be foveated in order of decreasing salience [44,45].

A recent study has provided evidence for the tight coupling of the oculomotor system with a sensory stimulus representation that is modulated by attention, that is, an integrated saliency map. Moore and Armstrong [46**] stimulated the frontal eye field (FEF) with currents too small to elicit eye movements while recording activity in area V4. They found an enhanced gain, that is, an increase in responsiveness, of neurons in V4 whenever the neuron's receptive field overlapped with the movement field of the FEF neuron. Although the artificiality of a

microstimulation experiment makes a separation of cause and effect difficult [47], these results nevertheless suggest a system in which planning eye movements to the most salient positions in the visual environment is tightly coupled to an attentional gain increase, in advance of the planned gaze shifts. In the process of this planning, attention will be shifted to one of the salient positions, enhancing the response of the affected neurons. This eccentric gain increase might bring about the activation of the FEF, which has not yet crossed the level at which a saccade is triggered, above threshold and trigger an eye movement, or it might fail to confirm the relevance of the potential target that is reflected in the saliency map. The evidence cited here for a central role of the FEF in the deployment of spatial attention corresponds well with findings on the role of the FEF as a stimulus salience area [48], with similar importance attributed to the lateral intraparietal area in the parietal cortex [26,49].

Conclusions

Our understanding of attentional influences has come a long way from the view that attention is a separable influence providing a late modulation of an otherwise stimulus-driven sensory information processing system. Instead, it appears that attention influences visual information even in the earliest areas of primate visual cortex. This influence seems to shape an integrated saliency map, that is, a representation of the environment that weighs every input by its local feature contrast and its current behavioral relevance. This map enables the visual system to integrate large amounts of information, even from outside the fovea, because it provides an efficient coding scheme for the potentially most relevant information in the sensory input. However, by completely integrating bottom-up sensory information and top-down attentional influences it equates the absence of attention with low stimulus power. This provides a possible explanation for the observation that highly salient stimuli will be processed even in the absence of attention, whereas low inherent salience will often prevent the perceptual representation of unattended parts of complex natural scenes [1], although exceptions seem to exist for basic categorizations, that is, a recovery of the 'gist' of natural scenes [50].

The brain areas that provide guidance for the top-down attentional effects seem to be tightly linked to those areas responsible for the planning and execution of eye movements, which is in agreement with the frequent need to foveate salient regions of the visual environment for a more detailed analysis.

Although many questions remain, the rapid advancement of functional imaging techniques and the development of sophisticated paradigms and recording techniques in monkeys trained to perform complex attentional tasks provides the basis for the growth in our understanding of

this area over the past few years. Bringing together bottom-up stimulus aspects that are often responsible for automatic attentional allocation and top-down influences that reflect voluntary attention, a global map representing stimulus saliency that is modulated by the current behavioral state of the organism can provide a unified framework for interpreting future findings on attentional effects and their close integration with sensory information processing.

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