Out of the spotlight: face to face with attention

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Figure-ground segmentation is a key early step in visual perception. A study now finds that V2 neurons in monkeys signal border ownership pre-attentively and that the effects of attention are predicted by the neurons' border preferences.

What you see is not always what you perceive. Perception is a creative process, and the human brain actively constructs the contents of our visual environment. An important first step in this process is the parsing of visual scenes into perceptual units, leading to the separation of figures from their background (**Fig. 1a**). Image segmentation is important because it constrains later processing. For example, figures are more likely to be selected for further processing than background elements. Do the neural processes related to segmentation operate automatically or are they susceptible to top-down influences? A recent study by Qiu *et al.*[1] in this issue demonstrates that figures are segmented into likely objects throughout the visual field independent of attention and that these object representations provide an interface for top-down selection.

Image segmentation is fundamental to object recognition, as it defines candidate objects that are later matched against known objects in long-term memory. Early twentieth-century Gestalt psychologists suggested several principles for segmentation[2]. As an example of the principle of good continuation, **Figure 1a** is perceived as two dark objects on a uniform light gray background, rather than as a gray object with two holes in it. They also noted that perception appears to assign contrast borders to objects (**Fig. 1**). Thus, the white square in **Figure 1c** seems to 'own' the border that it shares with the dark square.

Neural correlates of such Gestalt-based border ownership are found in secondary visual cortex (V2) and other extrastriate areas[3]. When an edge is placed in a neuron's receptive field (red circle in **Fig. 1b**), V2 neurons can differentiate whether the edge is part of an object border or part of the background. For example, even though the edge configuration in the receptive field is identical in **Figure 1a** and **1b**, a V2 neuron with this receptive field might fire more strongly for the configuration in **Figure 1b**, as the light region belongs to an object in **Figure 1b**, whereas it is part of the background in **Figure 1a**. Such neurons have been termed 'border-ownership neurons'.

These and other findings[4] indicate that figure-ground segmentation occurs early in cortical processing. To determine border ownership, V2 neurons must integrate contextual information from regions that are well beyond their small receptive fields. This requires global integration that might be mediated by local circuits in V2 or by a network that involves feedback from a higher cortical area with larger receptive fields, such as V4.

Qiu *et al.*[1] asked whether image segmentation occurs before or after attentional selection by investigating V2 neurons' border-ownership responses with or without attention. They recorded neural responses while monkeys carried out a shape-discrimination task. The animals were cued to attend to one of three simultaneously presented shapes and to indicate, with an eye movement or a manual response, whether the attended object was a target shape. One border of a shape was placed in a cell's receptive field; this border could belong either to the (attended) target stimulus or to one of the unattended shapes.

In agreement with previous findings[3], most V2 neurons showed border-ownership responses. These were found whether the border belonged to an attended or to an ignored shape. In addition, the timing of border-ownership responses were similar for attended and unattended figures. Although most neurons were modulated by both attention and border ownership, some cells only showed border-ownership modulation. Taken together, these results suggest that border ownership is calculated automatically and independent of attention. Thus, figure-ground segmentation is a pre-attentive process that occurs in a bottom-up, stimulus-driven fashion at early visual-processing stages. This helps to resolve a longstanding debate about the extent to which figure-ground segmentation is automatic.

The authors then looked at whether top-down attention interacts with border ownership. They used stimulus configurations with overlapping figures (**Fig. 1c**). For example, monkeys directed attention either to the white square or to the dark square, and neurons that preferred borders owned by the white square were recorded. Attention effects were larger when the white square was attended than when the dark square was attended. The sensory conditions in the neuron's receptive field were unchanged in the two attention conditions, but the attention effects could be predicted according to the neurons' border-ownership responses.

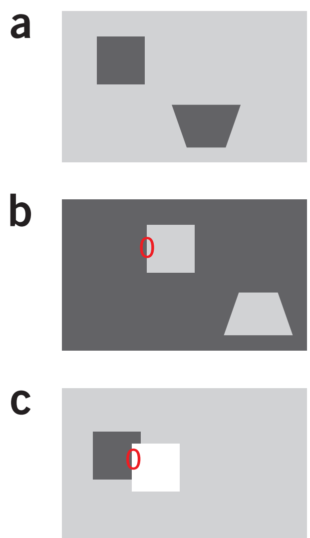

Figure 1 Figure-ground stimuli. (**a**,**b**) An example pair of stimuli used to investigate border-ownership effects. The local border contrast is held constant in **a** and **b**, and the objects are flipped about their edge. A border-ownership neuron (with a receptive field depicted as the red circle) will show a preference for a particular side of an object, firing more for configuration **b** than for configuration **a**, for example. (**c**) An example of the stimulus configuration used with overlapping figures. A neuron with a receptive field indicated in red is recorded while attention is directed to the white or dark square.

The authors propose an interface hypothesis of attention to explain these effects: the correlation between border ownership and attention may be explained by assuming that the same circuits underlie both processes and that the circuit that mediates border ownership provides an interface for attentional mechanisms. Thus, top-down mechanisms might operate on local circuits in V2 or on a V2-V4 feedback network during the selection of object information.

This hypothesis adds to a growing literature that challenges the traditional notion of attention operating as a spotlight[5]. The spotlight

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model assumes that attention enhances neural responses that are evoked by stimuli in a restricted region of visual space. Thus, the spotlight model predicts that the responses evoked by the edge configuration in the receptive field of **Figure 1c** should be equally enhanced when attention is directed to the white or to the dark square, as the receptive field is equally close to the focus of attention in both instances. However, in the new study[1], attentional modulation did not depend on spatial relationships, but instead depended on the neurons' border-ownership preference relative to the attended object. This agrees with human neuroimaging studies that show that attention can select not only regions of space, but also entire objects[6]. Therefore, border ownership is a likely neural substrate of object-based attention.

The idea that top-down processes act on local circuits or networks instead of individual cells might also help to resolve an ongoing debate about the role of attentional modulation in primary visual cortex. Single, isolated stimuli placed in the receptive fields of V1 neurons show little or no response modulation with attention[7]. However, greater attentional modulation is seen with more complex stimuli that provide context information[8,9]. The interface hypothesis may explain these discrepant findings. Complex stimulus arrays, but not single stimuli, engage local networks that represent context information, thereby providing the interface that is used by attentional mechanisms, resulting in robust attention effects. Thus, attentional modulation at a given processing stage in visual cortex may be best predicted by how much the attended stimulus engages local circuits. Also consistent with this idea, local interneurons (which subserve intrinsic circuits) receive stronger attentional modulation than other cell classes[10].

The interface hypothesis also converges well with the biased competition theory of attention[11]. When multiple stimuli are present at the same time in the visual field, they compete for neural representation in visual cortex. The neural substrate of this competition is a mutual suppression of neural responses[12], and this is another example of an automatic process that occurs without attention. When a stimulus is selected for further processing among multiple items, top-down processes appear to counteract the suppressive influences that are induced by nearby stimuli, and act to strengthen the neural representation of the attended stimulus[12,13]. These processes are typically observed at intermediate processing stages of visual cortex, such as in area V4 or MT. According to the interface hypothesis, these findings can be interpreted as competing stimuli engaging a local intrinsic circuit, thus providing an interface for the selection mechanisms to operate on. Thus, the interface hypothesis may provide a new framework for the interpretation of many empirical findings in the attention field.

In some respects, the interface hypothesis of attention is similar to another recent proposal[14]. Both hypotheses challenge the commonly held notion that attention acts in a hierarchical manner, which is based on the finding that attention effects are greater in extrastriate cortex than in early visual cortex. Instead, both proposals suggest that it is not a visual area's location in the processing hierarchy that determines the magnitude of attentional enhancement, but instead it is how involved the local circuits are in processing contextual scene information. The related proposal emphasizes the role of behavioral context, suggesting that a single visual area may perform many different functions depending on task demands. For instance, V1 neurons respond differently to the same visual stimuli depending on the type of behavioral task[14]. Attention is thought to gate the interaction of feedback connections from higher areas and local intrinsic networks, thereby strengthening connections that are important for the current behavioral context.

The idea that top-down selection mechanisms operate preferentially on intrinsic circuits and local networks not only provides an intriguing framework for explaining the role of top-down processes, but also raises a number of important issues that need to be addressed in future research. How do different interfaces, such as the segmentation circuit of early visual cortex and the competition circuit of later extrastriate cortex, interact[15]? Are the cellular mechanisms underlying attentional modulation of interface circuits the same across different visual-processing stages? Qiu *et al.*[1] have provided an important first step in revising some of our traditional notions of top-down selection mechanisms.

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The optimistic brain

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Faced with the metaphorical glass, most people see it as being half full. A new study shows that activity in two limbic areas, the rostral anterior cingulate cortex and amygdala, reflects an optimistic attitude.

Take a moment to consider the following questions. In uncertain times, do you usually expect the best? Do you expect more good things to happen to you than bad? Do you think that if something can go wrong for you, it will? Do you hardly ever expect things to go your way? People who respond "yes" to the first two questions and "no" to the latter two are characterized as optimists[1]. Most of us tend to be optimistic, which is a good thing because optimism is associated with many benefits to both physical and mental health; optimists tend to be well-adjusted psychologically and are equipped to handle stress well[2]. But we may be optimistic to a fault, in the sense that we maintain unrealistically positive expectations of our futures. For example, compared to the population in general, people think that they are more likely to own their own homes and live a long life and also think that

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