

versa for L2. Such an outcome would confirm the behavioral results of Clark et al. (2011) at the neuronal level and help clarify the relative role played by half-wave rectified (ON-ON, OFF-OFF) versus mixed luminance (ON-OFF, OFF-ON) channels along the L1/L2 pathways. Alternatively, it may be that HS cells are not the main determinants of the observed behavioral output, although earlier experiments generally suggested this to be the case (Pflugfelder and Heisenberg, 1995). Even though the models proposed by Eichner et al. (2011) and by Clark et al. (2011) are quite different, both of them reproduce a wide range of experimental data. This results from the inclusion of substantial nonlinear components and the emphasis on different contributions of L1 and L2 in motion processing. We are optimistic that in the near future, as these contributions are considered simultaneously, as additional experimental data become available and

additional cells in the circuit become genetically targetable, they will converge toward a unified picture of how *Drosophila* neural circuits implement the Reichardt correlation model. These are indeed exciting times for *Drosophila* and, more generally, insect vision.

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Searching for the Neural Mechanisms of Feature-Based Attention in the Primate Brain

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DOI 10.1016/j.neuron.2011.06.001

In this issue, two studies, one by Zhou and Desimone and another by Cohen and Maunsell, provide new insights into the mechanisms of feature-based attention (FBA). The former demonstrates a new role of the frontal eye fields in the origins of FBA and the latter shows that FBA is coordinated across both hemispheres.

The primate brain sensory systems have a limited processing capacity. For example, the visual system, comprising nearly 50% of the neocortex, can only effectively process a small percentage of the information entering the retinas at a given time (Van Essen et al., 1992). An effective solution to this problem has been to develop an attentional filtering mechanism that separates relevant from irrelevant incoming sensory signals in order to concentrate processing resources in the former. Two types of atten-

tional filtering have been identified—one driven by bottom-up (stimulus saliency) and the other by top-down (internal goals) cues. Decades of experimental work have also led to the identification of key structures and mechanisms that play specific roles in both types of attention. For the case of top-down attention, we have learned that the responses of neurons to visual stimuli in feature-selective and retinotopically organized visual areas of the macaque brain are strongly modulated when animals attend to a stimulus

feature or location. This has led researchers to classify the top-down attentional modulation of visual neurons response into feature-based (Treue and Martínez Trujillo, 1999), spatial (McAdams and Maunsell, 1999), and a third type called object-based attention (Roelfsema et al., 1998). One controversial topic in attentional research has been whether the two former types of attention share similar neural mechanisms. In this issue of *Neuron*, two different electrophysiological studies using advanced

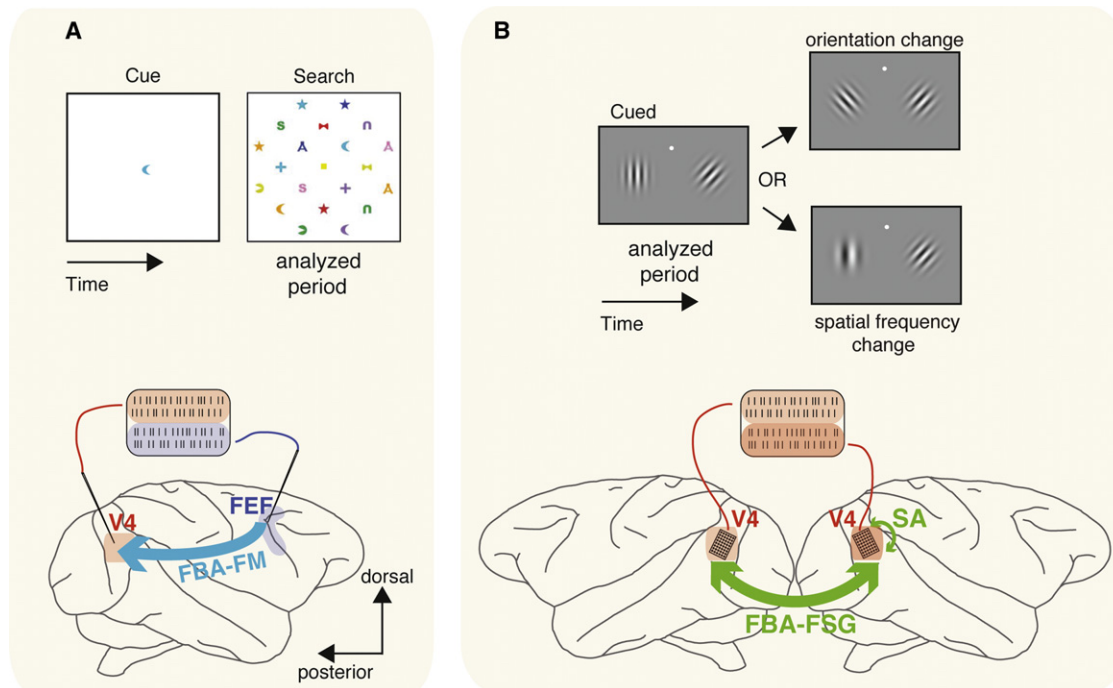


Figure 1. Mechanisms of Feature-Based Attention in Macaque Areas FEF and V4

Top: Zhou and Desimone (2011) (A) and Cohen and Maunsell (2011) (B) experimental designs (see original articles for details). Bottom: sketches with the summary of their main results. Multielectrode recordings are indicated by multiple single electrodes in (A) and multielectrode arrays in (B). The rounded rectangles symbolize the recordings (rasters) with the colors indicating the area (blue is FEF and red/orange is V4). FBA, feature-based attention; FM, feature matching; FSG, feature-similarity gain; SA, spatial attention. The turquoise arrow indicates signal flow from FEF to V4. Green arrows indicate correlated activity.

methodologies in behaving monkeys yield novel, complementary insights into this topic.

In the first study, Zhou and Desimone (2011) conducted simultaneous recordings from areas V4 and the frontal eye fields (FEF) of macaque monkeys during a visual search task that required the animals to memorize a visual cue presented at the beginning of a trial and then search, in a display composed of an array of different objects, for the one that matches the cue by directing gaze to single items (Figure 1A). Area V4 is located at a relatively early stage in the visual processing pathways and contains neurons selective for the color and shape of visual stimuli (Desimone and Schein, 1987). The FEF is located in the prefrontal cortex and contains neurons that encode the position of a visual stimulus, as well as the intended gaze position (Tehovnik et al., 2000). Some degree of shape selectivity has been reported in FEF neurons (Peng et al., 2008). Over the last decade, some studies have supported the role of the FEF as a source of top-down spatial attention signals that reach neurons in area V4 and modulate

their sensitivity to visual inputs (Gregoriou et al., 2009; Moore and Armstrong, 2003). So far, the FEF role in feature-based attention has remained unclear.

Zhou and Desimone (2011) found that during the visual search task, neurons in V4 and the FEF respond more strongly to the target stimulus or to stimuli sharing the target features than to other stimuli. The authors discarded the possible role of spatial attention by analyzing trials in which saccades were made to a stimulus away from the receptive fields of the recorded neurons. Because in these trials the focus of spatial attention was not on the stimulus inside the neurons' receptive fields but instead elsewhere at the position of the future saccadic eye movement, the authors conclude that the increase in response to stimuli matching the attended features was due to feature-based attention. Essential to their findings was that (1) the latency of this effect was shorter in FEF than in V4 neurons, and (2) the intensity of the response modulation was predictive of the efficiency of the visual search—as quantified by the number of saccades needed to find the target. This

demonstrates that the FEF is a potential source of top-down signals during tasks that require feature-based attention.

One interesting finding of the study is that feature-selectivity arose earlier in V4 than in FEF neurons. Thus, the FEF seems to combine incoming feature information from V4 with working memory signals carrying information about the relevant features to compute a saliency map that highlights the locations of potential targets. This map not only guides gaze but also provides feedback signals to V4 in order to enhance the processing of stimuli sharing the target color and/or shape (Figure 1A, bottom panel). Note that according to this hypothesis, although the trigger signal for the FEF saliency computation is a stimulus feature, the nature of the top-down signal is spatial, since it highlights locations of potential targets, i.e., it enhances responses of neurons with receptive fields that include stimuli resembling the target.

A difference between this and the previously proposed feature-similarity mechanism of attentional modulation is that here the attentional enhancement

occurs in neurons with receptive fields that include stimuli matching the target features (feature matching or FM [Motter, 1994]), rather than in neurons selective for the attended stimulus feature across the entire visual field (feature-selectivity gain or FSG, [Treue and Martínez Trujillo, 1999]). The distinction between these two alternatives can be made by measuring tuning curves for the different shapes and colors in V4 and FEF neurons and then determining whether the attentional enhancement occurred mainly in neurons selective for the target color or shape (FSG) or in any neuron containing a stimulus that matches the target feature within its receptive field, independently of the unit's selectivity for that feature (see Figure S6 of Zhou and Desimone [2011]). This distinguishes between a feature-based mechanism that combines feature and spatial information within a saliency map (FM) from another mechanism that combines information about the attended feature and the neurons selectivity (FSG). The study of Zhou and Desimone (2011) shows that neurons in the FEF are well suited to perform the computations underlying FM, and that the results of these computations guide visual search. The details of how different signals are combined within the FEF microcircuitry remain to be determined.

In a second study, also available in this issue of *Neuron*, Cohen and Maunsell (2011) implanted multielectrode arrays in V4 in both hemispheres of macaque monkeys and recorded the activity of single and multiple neurons during a task that required the deployment of spatial and feature-based attention. During the task, animals covertly attended to a stimulus at a cued fixed position in the visual field and detected a change in one of the stimulus features (orientation or spatial frequency). By introducing similar feature changes in a distracter stimulus presented simultaneously with the attended target and quantifying performance, the authors made sure that the animals correctly performed the task (Figure 1B). The effects of spatial attention could be isolated by comparing neuronal responses during trials in which the animals attended to the stimulus inside a neuron's receptive field versus trials in which the animals attended to an identical stimulus outside (McAdams and Maunsell, 1999).

Additionally, by alternating blocks in which the animals needed to detect orientation and spatial frequency changes they could compare responses when one or the other feature was attended and isolate the effects of feature-based attention (McAdams and Maunsell, 2000).

The authors found that populations of V4 neurons could independently show both types of attentional modulation. For example, a neuron could be modulated by spatial attention but not by feature-based attention and vice-versa. One main difference between the effects of spatial and feature-based attention was that the former enhanced responses of neurons within the hemisphere contralateral to the attended stimulus, while the latter enhanced neuronal responses in both hemispheres, irrespective of the attended stimulus location. The feature-based attentional modulation was dependent on the relationship between the attended stimulus feature and the cell's preferred feature (FSG, see Figure 2 of Cohen and Maunsell [2011]). For example, the response of a neuron when animals attended to a particular orientation was enhanced if the unit preferred that orientation but was suppressed if the attended orientation was antipreferred. FSG, as opposed to FM, produces enhanced or suppressed responses in neurons with receptive fields containing stimuli with the target features, depending on the units' feature selectivity (Treue and Martínez Trujillo, 1999).

Moreover, recording from 96 electrodes at a time (48 in each hemisphere) allowed the authors to examine the impact of spatial and feature-based attention on spike count correlations, a variable that has been shown to be influenced by the allocation of attention (Cohen and Maunsell, 2009; Mitchell et al., 2009). V4 units showing increases in response by both spatial- and feature-based attention show decreases in correlation, while V4 units showing response decreases by either type of attention showed increases in correlation. This suggests that response modulation and correlated firing are two sides of the same coin. Any variable that increases or decreases the firing rate of visual neurons to sensory stimuli (e.g., changes in contrast or adaptation) will likely produce decreases or increases in corre-

lated firing, respectively, and therefore will influence the ability of neuronal populations to encode visual information. Supporting this hypothesis, spike count correlations between pairs of MT neurons decrease when increasing stimulus contrast (Huang and Lisberger, 2009). The exact mechanisms of these effects need to be elucidated.

One important contribution of the Cohen and Maunsell (2011) study is demonstrating a correlation between the effects of spontaneous fluctuations in the two forms of attention at the level of neuronal population responses and behavioral performance. Moreover, fluctuations in the effects of feature-based but not spatial attention were coordinated across hemispheres. This suggests that spatial attention acts locally within a hemisphere, while feature-based attention operates globally across hemispheres (Figure 1B, bottom panel). It is unknown how this global feature-based modulation is implemented, but it likely involves a common input into areas V4 of both hemispheres from neurons that are feature selective. Zhou and Desimone's study, previously discussed in this article, may provide an answer to this question. Projections from feature selective neurons in FEF may target sensory neurons in visual cortex with similar preferences and produce the observed FSG effects. This would imply a role of the FEF in the origins of both FM and FSG effects. Another possibility is that other areas containing selectivity for stimulus features such as the neighboring dorsolateral prefrontal cortex (Zaksas and Pasternak, 2006) may provide top-down signals for the FSG modulation, since this type of attentional modulation does not seem to require the finer spatial resolution of the FEF map. These are important issues that need to be further investigated in future studies.

In summary, from these two studies we have learned that the mechanisms of feature-based attention are diverse and include different subtypes likely triggered by different task demands (e.g., FM during visual search, and FSG during detection/discrimination involving sustained covert attention). Moreover, the FEF, a structure involved in spatial attention, seems to play a role in FM during visual search. The mechanisms producing the global effects of FSG remain, so far, unknown.

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