

TINS special issue: The Neural Substrates of Cognition

Feature-based attention in visual cortex

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Although most studies of visual attention have examined the effects of shifting attention between different locations in the visual field, attention can also be directed to particular visual features, such as a color, orientation or a direction of motion. Single-unit studies have shown that attention to a feature modulates neuronal signals in a range of areas in monkey visual cortex. The location-independent property of feature-based attention makes it particularly well suited to modify selectively the neural representations of stimuli or parts within complex visual scenes that match the currently attended feature. This review is part of the *TINS* special issue on *The Neural Substrates of Cognition*.

Introduction

Visual attention is a powerful mechanism that enables perception to focus on a small subset of the information picked up by our eyes. This modulation of bottom-up signals enhances the representation of behaviorally significant portions of the input at the expense of those aspects deemed less relevant. This notion of selection is captured in the popular metaphor of attention as a spotlight, in which those spatial regions falling within the current focus of attention receive enhanced processing. Space-based attention has dominated investigations of attention, and has been the subject of recent reviews [1–3]. However, attention can be allocated not only to a particular location but also to a particular feature. Although such feature-based attention has received less study than space-based attention, results from recent single-unit experiments suggest that they rely on closely related mechanisms.

Feature-based attention – that is, the ability to enhance the representation of image components throughout the visual field that are related to a particular feature – should be particularly useful when searching for a stimulus with that feature. This ability to detect such a target – a behaviorally relevant item – among distractor items is the basis of a very popular paradigm in visual psychophysics: visual search. In visual search experiments, targets and distractors differ by at least one feature, such as their color or orientation, and the target is typically defined in advance of the presentation of the search array. Whether subjects detect a target using

a parallel search process or using a serial process that guides a recognition mechanism through a sequence of potential target locations [4], target detection could be improved by enhancing the representation of image components that match the attended feature (e.g. the color red or a vertical orientation) and by suppressing those that do not. One approach to achieve such modulation would be to employ feature-based attention to enhance the responses of all neurons that respond preferentially to the attended feature, thereby selectively strengthening the representation of stimuli sharing the attended feature before any stage where objects are recognized.

Many psychophysical studies have demonstrated that feature-based attention improves detection or otherwise enhances behavioral performance across the visual field (e.g. Refs [5–9]). Neural correlates of feature-based attention were identified in some of the earliest brain-imaging studies [10] and continue to be actively investigated in functional magnetic-resonance imaging (fMRI) studies [11–16]. We focus here on evidence from single-unit recordings made in the visual cortex of macaque monkeys, which have provided detailed insights into how feature-based attention alters the neuronal representation of the visual scene.

Single-unit electrophysiology of attentional modulation in visual cortex

Most single-unit studies of attention have been done at intermediate levels of the hierarchy of visual cortex, such as area V4 in the ventral pathway and the middle temporal visual area (MT) in the dorsal pathway. These areas are frequently examined not because they are thought to have a special or prominent role in attention, but because they represent a good compromise between earlier stages of the visual pathways, where neurons respond robustly and predictably to simple stimuli and have moderate-sized receptive fields, and later stages in the pathways, where the effects of attention tend to be more pronounced [17].

Dozens of single-unit studies have examined the effects of space-based attention on responses in visual cortex. An important result from these studies has been that space-based attention changes the strength of neurons' responses without changing their underlying response properties. This multiplicative modulation increases the responses of neurons in V4 without systematically sharpening or broadening their orientation tuning curves:

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responses to all orientations are scaled proportionally [18]. Spatial attention similarly increases the response gain in MT without affecting the width of direction tuning [19] and does not change the trial-to-trial variance of responses [20]. Additionally, spatial attention has been shown to enhance synchronization of neuronal activity and this enhanced synchronization correlates with enhanced neuronal and behavioral responses to changes in attended stimuli [21,22]. In contrast to this body of knowledge on spatial attention, relatively few single-unit experiments have focused on feature-based attention.

Feature-based attention in V4

Most single-unit studies of feature-based attention have examined V4, which is implicated in form recognition and visual search [23,24]. Modulation of V4 responses by space-based attention has been demonstrated many times [18,25–29]. Haenny *et al.* [30] provided one of the first demonstrations of feature-based attention in V4. Monkeys were shown a series of visual gratings and were trained to respond when they saw a grating that matched the orientation of a cue grating that was presented at the start of the trial. More than half the neurons recorded in V4 had responses that varied depending on which orientation the animal was seeking. This modulation by target orientation is also seen if the animal is cued by having it feel the orientation of a grooved plate or bar that it cannot see [30,31], suggesting that feature-based attention is mediated by centers that are capable of generating an intermodal representation of orientation.

Motter [32,33] trained monkeys to do a task in which they viewed arrays of mixed stimuli and had to attend to a subset of stimuli with a color or luminance that matched a cue stimulus. Most of the responses recorded from V4 neurons were stronger when the stimulus in their receptive field matched the cue. Although this modulation was based on the visual feature that the animal was attending to, this task represents an example of a study where spatial attention might have had a role: it is possible that the change in neuronal activity depended on a mechanism that targeted spatial locations identified by the animal as behaviorally relevant based on color or luminance.

McAdams and Maunsell [34] showed effects of shifting attention between feature dimensions, rather than specific values of a given feature. Responses were recorded from V4 neurons with a stimulus of the preferred orientation in their receptive field. In one condition the animal was required to attend to the orientation of another stimulus in a distant location. In a second condition the animal was required to attend to the color of an unoriented stimulus in the distant location. The responses of most V4 neurons were affected by shifting attention between orientations and colors. This result showed that the neural representations of stimuli in parts of the visual field that have no relevance to the task are modulated by feature-based attention. Effects of feature-based attention remote from the locus of spatial attention are consistent with the idea that feature-based attention changes activity throughout the visual-field representation in a way that would be useful for visual search.

Feature-based attention during visual search

Visual search is one task where feature-based attention should be particularly valuable. Several studies have shown that neuronal responses vary in predictable ways depending on whether the animal was attending a preferred feature of the recorded neuron. Chelazzi and colleagues [35,36] showed that the activity of individual V4 and inferotemporal neurons is modulated when monkeys search for different targets. For each neuron they recorded, they identified two images. On each trial they cued the animal to respond to one of two stimuli presented within the receptive field of the neuron: one that generated a relatively strong response and one that generated a relatively weak response. Shortly before the animal responded, neural activity was stronger when the searched-for stimulus was the preferred stimulus of the neuron. Although these findings are consistent with feature-based attention, a more parsimonious explanation accounts for the observed modulation by spatial attention. The enhanced response to preferred stimulus targets shortly before the monkey signaled its choice would then be the 'spotlight of attention' of the animal, enhancing the effectiveness of the attended stimulus at the expense of representation of the distractor.

In a recent study, Bichot *et al.* [37] were able to avoid this alternative explanation for attentional modulation during a visual search task. Monkeys were trained to search for a target with a particular color or a particular shape in a crowded display (Figure 1a) and were allowed to move their gaze freely. Responses were recorded during the brief periods between saccades, when a known stimulus lay in the receptive field of the neuron being recorded. The critical responses were those recorded when the target stimulus fell in the receptive field of the neuron being recorded but was not detected by the animal, who made an eye movement elsewhere and continued the search. These responses were compared directly with those recorded in other trials in which the same stimulus was a distractor. Almost all the neurons examined gave a larger response when the stimulus in their receptive field matched the cued feature, with a median increase of 30% (Figure 1b). Bichot *et al.* also looked at the effects of attention on the local field potential (LFP). Although the responses of individual V4 neurons were affected by feature-based attention, there was no effect on the magnitude of the LFP. However, the coherence between the spikes of individual neurons and the LFP increased in the gamma band (30–60 Hz) when animals searched for the stimulus preferred by neurons at the recording site. Thus, feature-based attention matches spatial attention, for which influences on the synchrony of neuronal firing have been documented [21].

Feature-based attention in MT

The aforementioned experiments were all done in the ventral visual pathway, primarily in V4. Robust effects of attention to features have also been seen in the dorsal pathway. Martinez-Trujillo and Treue [19,38] examined attentional modulation in MT, which is important in the perception of visual motion [39,40]. In one experiment, a stimulus inside the receptive field moved in the preferred

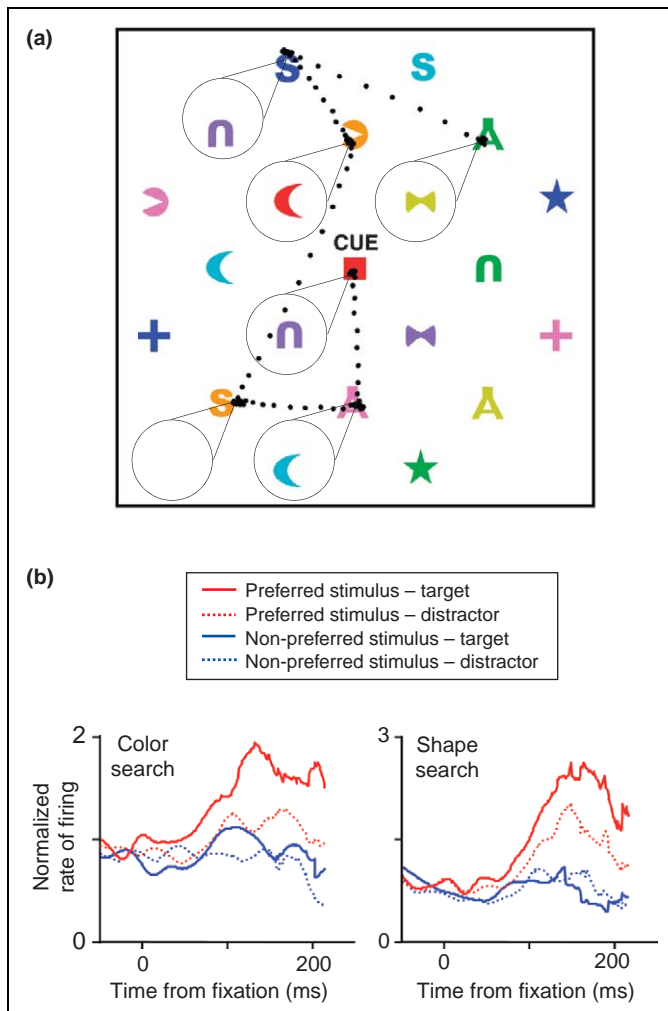


Figure 1. Visual search task. **(a)** One trial of a color-search task. A central cue indicated the target color, which the animal then searched for by making a sequence of saccades (dotted lines) within the array. Each saccade moved the receptive field of the neuron being recorded to a different part of the display (circles). The critical measurements were made when the target stimulus (a red crescent in this case) fell in the receptive field, but the animal failed to detect it and made an eye movement to another stimulus. These responses were compared with responses to the same stimulus when it fell in the receptive field during trials in which it was not the search target. **(b)** Average normalized responses of V4 neurons during search. The red lines show the average response to a preferred stimulus during search trials when it was the search target (solid lines) or when it was a distractor (broken lines). Blue lines are equivalent data for non-preferred stimuli. Neurons responded more strongly to preferred stimuli when the animal had been cued to search for those stimuli. This enhancement was seen for both color searches and shape searches. Excerpted, with permission, from Ref. [37] © (2005) AAAS.

or null direction while the animal attended to a distant stimulus that could also move either in the preferred or null direction. Martinez-Trujillo and Treue found that the change in the direction of motion that the animal was attending modulated the response to the behaviorally-irrelevant stimulus in the receptive field. When attending to motion in the preferred direction responses were on average 13% stronger. This modulation was similar in size to that seen in V4 [34], suggesting that the same feature-based attention system acts in both pathways.

Furthermore, as has been described for spatial attention, feature-based attentional modulation seems to be multiplicative, causing a gain change of the affected neurons that increases responsivity whenever attention

is directed to the preferred direction of a neuron and decreases responses when attention is on the anti-preferred direction. An important corollary of this result is that attention to a particular direction does not increase the responses of all neurons to that direction. To the contrary, attending anywhere in the visual field to a direction that is the null direction for a neuron will, on average, reduce its responses to any direction inside its receptive field (Figure 2).

The similarities between feature-based and space-based attention raise the possibility that they are simply different sides of the same coin. This has led to the 'feature-similarity gain model' proposed by Treue and Martinez-Trujillo [19], in which the change in gain of a visual neuron depends on the similarity of the features of the current behaviorally relevant target and the response selectivities of the neuron. Similarity might be based on the spatial location or any other feature. Thus, responses would be enhanced for all neurons whose sensory selectivity matched the current attentional state (i.e. feature-similarity for the non-spatial feature); similarly, independent of their stimulus selectivity, responses would be enhanced of all neurons whose receptive fields overlapped an attended location in the visual field (i.e. feature-similarity for location).

It is worth noting that in this scheme, stimulus properties determine the basic sensory response of a neuron but not the sign or magnitude of the attentional modulation. The modulation is a gain change that is independent of the stimulus driving the neuron – in fact, a stimulus is not even needed, neither in the receptive field (because most neurons show some firing even in the absence of any stimulus) nor at the attended location (as long as the subject is allocating attention even without a stimulus to focus it on). This can account for the attentional modulations that have been reported in the absence of sensory stimulation [28,41]. This general framework can explain a wide range of effects of attention on single-unit responses [42].

Putting it all together

Combining the insights gained from studies of space-based and feature-based attention, it is possible to infer the attentional modulation of a population of neurons that have receptive fields at various positions and prefer various values for a particular feature (e.g. orientation in V4 neurons or direction of motion in MT) that will occur when attention is directed to a particular stimulus feature at a particular location in a complex visual scene. Let us imagine a scenario where the visual input creates a fairly homogeneous level of activation across the neuronal population. Spatial attention will increase the gain of all neurons whose receptive field overlaps the current attentional focus, creating an enhanced representation at that location that is akin to a local increase in contrast [41,43] and that creates a corresponding perceptual effect [44]. Note that according to the feature-similarity hypothesis this modulation of the retinotopic population would produce a range of gain changes, because neurons whose receptive fields only partially overlap the focus of attention would experience a smaller gain increase than

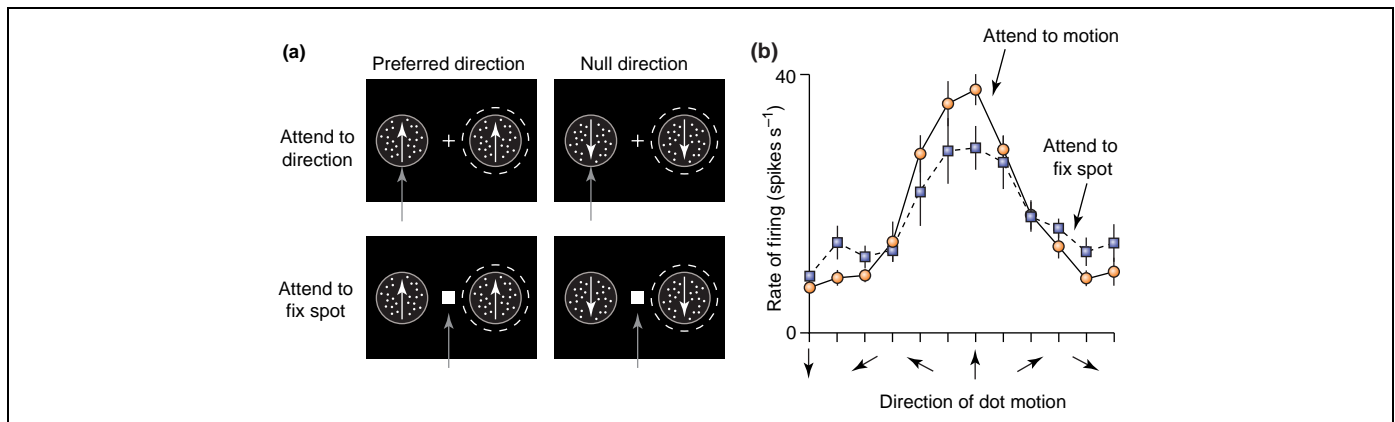


Figure 2. Feature-based attention in MT. (a) Schematic representation of tasks used to assess the effects of attention to direction of motion. Two patches of random dots were presented, one within the receptive field of the neurons being record (broken white line). The patches always moved in the same direction (white arrows), but different directions of motion were presented on different trials. On some trials (lower row) the attention of the animal (gray arrows) was directed to the fixation spot to detect a change in luminance. On other trials (upper row), a cue at the beginning instructed the animal to pay attention to the motion of the patch outside the receptive field to detect a change in that motion. (b) Responses of a representative MT neuron to different directions of motion during the two states of attention. Attention to the preferred direction of motion increased the response of the neuron, but attention to the null direction of motion decreased its response. Thus, attention to a particular direction of motion does not increase responses across all neurons. Rather, it has a push–pull effect that increases responses only for neurons that prefer motion close to the attended direction. Reproduced, with permission of Elsevier, from Ref. [38].

those centered on the focus, a prediction that has not been tested experimentally.

In addition to this modulation at the focus of attention in the retinotopic representation of the visual input, the attended non-spatial feature will cause further modulation. This will exert a differential gain change across the whole retinotopic representation, with a particularly strong gain increase for neurons preferring the attended feature and a gain decrease for those of opposite preference. The total effect will be a population response that is no longer homogeneous but has its highest activity in the group of neurons preferring the attended location and feature, intermediate enhancements at retinotopic locations where the visual input matches the attended feature (i.e. potential targets in a visual search situation), and suppressed responses everywhere else. Combining such modulated population responses across cortical areas could create an integrated saliency map –that is, a topographic representation of relative stimulus strength and behavioral relevance across visual space [45].

Wiring up attentional modulation

Creating complex differential attentional effects across a population of neurons raises the question of how this can be achieved by top-down input from centers responsible for the allocation of attention. For space-based attention, one could imagine a specialized visuotopic map that represents which parts of visual space are currently of greatest behavioral relevance: an attention map. Such a representation of behaviorally relevant locations might be activated by knowledge of the environment, or by interactions between such knowledge and current sensory signals [46]. Excitatory connections between sites in a visuotopic map of attention and visual cortex neurons that have receptive fields in corresponding locations might mediate modulations of sensory responses by space-based attention. Functional imaging studies have identified topographic organization related to spatial attention in parietal and frontal cortex that might serve this purpose [47,48]. In a recent study, Moore and Armstrong activated

what seems to be part of such a system when they microstimulated the frontal eye field (FEF) and observed retinotopically matched enhancements in V4 that resembled those observed in attentional studies [45,49].

It is more difficult to envisage the implementation of feature-based attention. Whereas spatial attention involves the two (or possibly three [50,51]) dimensions of visual space, a subject might pay attention to any of a potentially enormous number of stimulus features. The brain might be unable to maintain neurons devoted to representing the behavioral relevance of each these features. The FEF-stimulation study suggests that a spatial map of attention might be used to enhance the responses of neurons throughout the visual cortex that had receptive fields overlying the attended location. An analogous arrangement for feature-based attention would require representations for each feature that might be attended (e.g. orientation, color, curvature, patterns or shapes), such that activation of such a representation (reflecting the allocation of attention to a particular feature value) would modulate the activity of neurons throughout visual cortex that were selective for the particular feature.

Maintaining the analogy to the control of attentional modulation exerted by spatial attention onto sensory areas, two issues emerge. First, efficient implementation of top-down control of feature attention might require a topographic organization for the attended feature and a systematic tuning of sensory neurons along the feature. For spatial location, these requirements are fulfilled by the retinotopic organization and the well-defined spatial receptive fields in early areas of the visual pathways. A topographic organization has been documented for some stimulus features, such as motion direction and stereoscopic disparity [52,53], but it is not known whether representations of most features are topographically organized. Furthermore, for neuronal representations of complex features in inferotemporal cortex, it is not even clear what the tuning dimensions might be [54–58].

Second, an important constraint might be the numbers of neurons that would be needed to represent the behavioral relevance of all features. If the attentional resolution needs to be high, it seems reasonable to assume that the representation of the behavioral relevance of a feature would require as many neurons as contribute to the sensory representation of that feature. If so, then the behavioral relevance of some features could be represented efficiently, but for others we lack the data for such an estimate. For example, the behavioral relevance of low-level features represented in V1 (e.g. orientations or colors) might be accomplished by a hypercolumn-sized piece of cortex. This is because each hypercolumn in V1 contains a complete representation of the encoded features, with the other hypercolumns replicating this representation for other retinal positions. Applying such an estimate to the features represented only in higher areas of extrastriate cortex seems currently impossible given the lack of understanding about feature representations in those areas.

It is possible that representing the behavioral relevance of all the features represented in visual cortex would require more neurons than the brain could afford. Therefore, a crucial question is what limits there are on the types of features to which one can direct attention. To our knowledge, no experimental evidence addresses the capacity of feature-based attention. Feature-based attention, and the neuronal representations on which it depends, might be limited to a subset of features that frequently demand attention, such as colors and orientations, and might not work for all features that are readily discriminated. Studies that investigate which features are topographically represented might provide important insights. With plasticity, it might be possible to reserve the ability to generate representations that might support attention to any feature, or perhaps combinations of features, after practice. Behavioral improvements in searching for certain patterns following practice [59] are consistent with this idea. It will be important to learn more about the limits of feature-based attention as we try to understand how attention is implemented in neuronal representations.

Closing comments

In summary, feature-based attention is a mechanism that modulates sensory responses across the visual field. Its similarity with spatial attention suggests a unified attentional system that treats the location of a stimulus as one of its features. This system would be able, without the need to rely on a sophisticated preliminary analysis of the input (e.g. object segmentation and recognition, or long-range stimulus comparisons), to create a representation of the visual environment that enhances aspects that match the current behavioral preference, at the expense of the vast portion of the input that is behaviorally irrelevant. Such a representation is an important component for a visual system that needs to concentrate its limited processing resources on the most relevant sensory inputs.

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