Neural basis of visual selective attention



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Attentional modulation along the object-recognition pathway of the cortical visual system of primates has been shown to consist of enhanced representation of the retinal input at a specific location in space, or of objects located anywhere in the visual field which possess a critical object feature. Moreover, selective attention mechanisms allow the visual system to resolve competition among multiple objects in a crowded scene in favor of the object that is relevant for the current behavior. Finally, selective attention affects the spontaneous activity of neurons as well as their visually driven responses, and it does so not only by modulating the spiking activity of individual neurons, but also by modulating the degree of coherent firing within the critical neuronal populations. © 2010 John Wiley & Sons, Ltd. *WIREs Cogn Sci*

INTRODUCTION

V isual selective attention acts as a key mechanism aiding efficient object recognition, perceptual awareness, goal-directed behavior, and selective memory storage. The most natural and widespread expression of visual selective attention is when individuals turn their gaze toward a salient or otherwise interesting object in their surroundings, in order to align it with the high-resolution fovea of the retina,¹ which allows more detailed processing of the fixated object at the expenses of competing objects falling on peripheral regions of the retina. However, it is well established that selective attention can be aimed at extrafoveal locations and objects, thus effectively decoupling the high-resolution power of the fovea from enhanced brain processing due to selective attention.²

There appear to be several computational reasons why the brain implements selective attention mechanisms. First and foremost, selective attention can be viewed as the mechanism that mediates choice of the next target for preferential, foveal analysis, thereby primarily assisting the oculomotor system to optimize sensory sampling of the visual environment,

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given the current goal and priorities established through evolution.^{3,4} Second, selective attention is needed to focus processing onto a single object in order to plan coherent behavioral responses targeted at the selected object, as motor systems in general, including those for reaching and grasping movements, are physically constrained and can only act on one (or a few) objects at any given moment.⁵ Third, selective attention is necessary to gate access of perceptual representations to memory systems, as it is probably impossible, or perhaps simply disadvantageous, for the memory systems of the brain to store each and every single object and event occurring within a busy environment.^{6,7} Finally, selective attention is needed to allow entrance of the selected representation into working memory and conscious perception, as perceptual awareness is inherently limited in nature, and it unfolds serially, with a single percept (or inner content) gaining dominance at any instant in time.^{8,9}

Above and beyond the previous explanations, students of vision and selective attention raise two further related reasons as to why selective attention may be indispensable. One reason is that processing of incoming retinal input must be focused on a single object at a time simply because otherwise simultaneous processing and recognition of all objects would overcome the limited processing capacity of the visual system, a point further elaborated below.^{10,11} In addition, and more specifically, directing attention toward a single object at a time might serve the important function of aiding the correct conjoining of elemental features belonging to the object, therefore

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preventing the erroneous binding of features belonging to separate objects in a cluttered scene.^{12,13} In brief, as stated at the beginning, selective attention appears to be a key mechanism for efficient object recognition, perceptual awareness, goal-directed behavior, and selective memory storage.

An important distinction should be made at the outset. When speaking of selective attention, one should differentiate between the effects and the causal control mechanisms. Specifically, one may use the term 'selective attention' to refer to the modulation of sensory-perceptual processing along the visual system in relation to concurrent changes in behavioral performance, in which case the term would index the effects of visual selective attention at the neuronal as well as at the behavioral level.¹⁴ In contrast, one may use the term to refer to the signals that, within a given behavioral context, bring about the attentional effects considered above.¹⁵⁻¹⁷ The available evidence suggests that in most cases these signals originate outside the visual system proper.¹⁸⁻²¹ This review mainly concentrates on the effects, or manifestations, of selective attention, while some of the available evidence regarding causal control mechanisms will be briefly addressed in the last section of the article.

Given the key role of selective attention in visual processing, in particular, its role in building and gating object representations, it comes as no surprise that much of the relevant experimental work over the past three decades has been devoted to the investigation of the neuronal correlates of selective attention along the ventral, object-recognition pathway of cortical visual processing.^{14,22,23} The ventral pathway originates at the level of primary visual cortex, or V1, and nearby secondary visual cortex, or V2, and further extends through extrastriate area V4 and posterior inferotemporal (IT) cortex, or area TEO, to culminate in a relatively vast cortical territory occupying the middle and anterior segments of the IT cortex. The ventral pathway represents a network of interconnected areas, mostly organized according to a hierarchical scheme, but also heavily characterized by a reverse hierarchy of re-entrant signals, whereby object representations are synthesized with an ascending level of complexity and representational invariance.²⁴ Ultimately, patterns of activity within IT cortex are now known to encode with remarkable speed and efficiency the various objects we are able to recognize. Key nodes along this pathway are represented by area V4 and the various sectors of IT cortex, and therefore this article will focus on these nodes of the pathway.

Several forms of selective attention are distinguished here, including enhanced processing of

individual attended items, selective processing among competing items (or biased competition), featurebased guidance of target selection in visual search, object-based attention, and, finally, feature-selective attention.

ENHANCED PROCESSING OF ATTENDED OBJECTS

Psychophysical studies on human observers have documented robust effects of attention on visual sensitivity at selected regions of space. Sensitivity has been shown to increase at attended versus unattended locations in the visual field, with relatively shorter reaction times to detect an item at the attended location, as well as greater accuracy.^{2,25} In particular, attentional facilitation entails better detection of faint, low-contrast stimuli, and improved discrimination of their features,²⁶ as if attention to the stimulus led to the enhancement of signal strength.²⁷ In turn, these effects are reminiscent of those produced by an increase in stimulus contrast, and it has been reported recently that indeed attention increases perceived stimulus contrast.²⁷ Consistent with these behavioral results, single-unit recording studies in the behaving macaque have found enhanced neuronal responses to a single stimulus presented inside the receptive field (RF) of the given neuron when the animal's attention is aligned with the stimulus location, relative to when attention is directed elsewhere in the visual field. As a result, stimuli at an attended location engender stronger central representations than unattended stimuli do. These neural effects likely represent part of the mechanism underlying enhanced behavioral performance, as previously described. Spatially directed attention has been shown to enhance neuronal responses to a single stimulus in the RF at nearly all levels along the ventral pathway of the visual system, including area V1,²⁸ area V2,^{28,29} and area V4.^{28–32} Nonetheless, there is also evidence to suggest that the magnitude of attentional enhancement increases as one ascends the visual hierarchy.²⁸ Analogous modulatory effects of attention have been demonstrated in visual areas of the dorsal stream, such as MT and MST.³³

It has recently been reported that spatially directed attention also affects neuronal firing prior to the cortical level. In particular, enhanced visual responses due to selective attention were found in the lateral geniculate nucleus (LGN) of the thalamus, including both magnocellular and parvocellular layers, whereas decreased responses were concurrently obtained in the thalamic reticular nucleus (TRN).³⁴ As the TRN receives excitatory input from the LGN, in

turn exerting on the LGN a powerful inhibitory influence, the attention-dependent suppression described for TRN neurons lends itself to the intriguing possibility that a decreased inhibitory influence exerted by this nucleus may contribute directly to enhanced visual responses in the LGN.³⁴

Regardless of this pervasive influence across the visual pathways, overall, enhancement of neuronal responses to individual stimuli presented inside the RF is not very strong, typically on the order of 20% or less along the ventral pathway.³¹ Furthermore, the effect has not been found under all experimental conditions,^{29,32,35} and a possible account of this inconsistency is offered below.

Recent studies of neuronal responses in area V4 have shed further light on the above modulation of responses to single RF stimuli as a function of attention. If the effects of attention on perceptual performance, as previously described, are akin to those brought about by increased stimulus contrast, then one might predict that directed attention changes the contrast response function of neurons. Neurons in the visual system typically produce increasing responses as a function of stimulus contrast, up to a plateau, and the function takes the form of an H-ratio function (similar to a sigmoid).^{36,37} If attention acts by increasing the effective contrast of the RF stimulus, then one predicts a leftward shift in the contrast response function of the neurons (Contrast Gain Model³²). In line with this prediction, attention directed to the RF stimulus was found to cause a leftward shift of the function relative to when the stimulus was unattended.^{32,38} As a consequence, responses to an attended stimulus will not differ from those to an unattended stimulus at or beyond the point of saturation in the contrast response function. Instead, effects of attention will be greatest within-or just below-the dynamic range of the contrast response function for the given neuron. These findings may explain, at least in part, why not all single-cell recording studies have obtained enhanced responses to attended compared with unattended single RF stimuli along the ventral pathway, including area V4, as attentional effects may be minimal, if any, when stimuli of high contrast are employed. In summary, prevailing evidence indicates that stimuli presented at attended locations will elicit greater responses compared to stimuli at ignored locations. However, the effect is relatively large with stimuli of low contrast, whereas it tends to decrease with increasing contrast of the stimulus.

Notice, however, that there is an important difference between the effects of directed attention and contrast on responses of neurons in visual cortex, including area V4. Namely, while attention mimics the effect of contrast in terms of response magnitude, it does not do so in terms of response onset latencies. Response latency has been shown to increase considerably for low-contrast stimuli,^{37,39} whereas no detectable change in response latency is associated with manipulations of attention.^{32,40} This imposes some caution in likening effects of attention to changes in effective stimulus contrast.

Moreover, the appealing notion of a tight correspondence between the effects of attention and the effects of increasing stimulus contrast was challenged by results showing a multiplicative effect of attention on contrast response functions.⁴¹ Namely, according to this work, attention will increase neuronal firing by applying a fixed gain factor, which simply rescales the entire contrast response function of the neuron, with largest absolute effects occurring at the plateau (Response Gain Model).

A computational model, the Normalization Model of Attention,^{42,43} has recently been proposed to try and reconcile such apparent discrepancies. In simple terms, the model—which is an elaboration of a pre-existing model of neuronal visual processing--posits that the excitatory stimulus drive impinging on a single neuron is normalized (divided) by the sum total drive across the neuronal population (suppressive drive). The effect of attention in the model is to multiply the excitatory drive for the neuron in a selective manner, prior to the impact of normalization. The model succeeds at predicting different effects of attention on neuronal firing (i.e., either a change in contrast gain or a multiplicative scaling of the contrast response function), as reported in the literature, by taking into account the specific sensory conditions (e.g., type and size of the RF stimulation) and the degree of attentional focusing. Although the model must await direct validation from future empirical evidence, it has the indisputable merit of proposing a unitary theoretical framework to account for a large variety of observations in the literature.

An important question is whether directed attention, in addition to changing the strength of neuronal responses, will also modify neuronal tuning for the stimulus features, for example, stimulus orientation. This has been addressed in a number of studies and the prevailing notion is that tuning properties of neurons are relatively immune to the influence of spatially directed attention³¹ (however, attention-dependent sharpening of tuning has been reported under difficult task conditions⁴⁴), although they may be modified as a result of extensive discrimination training with perceptual learning protocols.⁴⁵ Instead, spatially selective attention has been shown consistently to cause multiplicative scaling of tuning curves. Therefore, responses throughout the tuning curve will be multiplied by a constant factor, with no appreciable changes in the filter properties of neurons.³¹ Again, this is similar to the known effect on tuning curves of varying stimulus contrast.⁴⁶ Nonetheless, it is conceivable that a gain modulation of tuning curves allows finer encoding of features at an attended versus unattended location, for instance, by increasing the signal-to-noise ratio at the attended location. For example, by exclusively enhancing visual responses without affecting response variability, attention can increase the signal-to-noise ratio of the neuron, as the signal grows comparatively more than the noise, consequently improving stimulus discrimination capacity.⁴⁷ Additionally, as we will develop further in this section, an increase of the signal-to-noise ratio could also result from a significant reduction in the variance of responses to attended versus unattended stimuli.48,49 More importantly, as detailed below, attention may strongly improve the signal-to-noise ratio of the pooled neuronal signal by de-correlating response variability across neurons in the population.49,50

Researchers have also provided evidence that the RF profile may change under the influence of attention in area V4, typically shifting in the direction of the attentional focus,³⁰ and similar findings have been reported for area MT along the dorsal pathway.⁵¹ However, the question remains as to whether what can be described as a shift of the RF depending on the direction of attention is not the simple consequence of relatively enhanced responses at or near the focus of attention and progressively weaker responses at increasing distances from the focus.

A recent development in the field has concerned the investigation of differential attention-dependent modulation of responses in separate classes of cortical neurons, in an attempt to characterize the microcircuitry that gives rise to attentional effects.⁴⁸ Specifically, two cell classes have been distinguished in area V4 based on the waveform (duration) of their action potentials-a parameter that has been shown previously to vary across distinct classes of neurons in intracellular recording studies.⁵² Narrow-spiking neurons, believed to correspond to inhibitory interneurons, showed greater attentional effects than broad-spiking neurons, likely corresponding to excitatory pyramidal cells. In particular, narrow-spiking neurons displayed not only relatively more enhanced responses in absolute terms, but most importantly a larger reduction in the variance of responses to attended stimuli, which in turn should increase the reliability of these neurons with regard to stimulus encoding capacity.⁴⁸ The intriguing observation that the largest effects of attention were found for candidate inhibitory interneurons may be consistent with the conjecture that these neurons play a crucial role in mediating suppressive effects onto distracting, nearby stimuli and in the modulation of response synchronization.⁴⁸

A further emerging development toward a better understanding of the neuronal interactions that give rise to attentional modulation of responses in visual cortex has been recently pioneered by studying the specific role played by some of the major neurotransmitter systems. For example, Herrero et al.⁵³ directly tested the contribution of acetylcholine (Ach) to attentional effects in area V1, by combining ionthophoretic delivery of cholinergic drugs with single-cell recordings in the behaving macaque. In their study, like in previous reports, spatially directed attention determined enhanced responses when attention was directed to the RF location. This attentional modulation was magnified by local Ach injection, which also resulted in a significant effect at the behavioral level, with a greater RT difference between the attended and the unattended condition. Conversely, the attentional modulation was reduced by the local injection of the muscarinic antagonist scopolamine, whereas no systematic effect was found with the nicotinic antagonist mecamylamine, thus suggesting a specific role of muscarinic cholinergic mechanisms in mediating the attentional effects in V1.53 Additional investigation will be crucial in order to extend these findings to other cortical visual areas. Moreover, it will be essential to fully establish whether muscarinic cholinergic mechanisms have a specific role in mediating attentional effects or whether any effect on attention is mediated by a more general 'energizing' effect of cholinergic neurotransmission on cortical processing. Very recently, Goard and Dan⁵⁴ performed a study in which they electrically microstimulated the nucleus basalis of the basal forebrain-the origin of widespread cholinergic projections to the neocortex, and concurrently recorded neural activity in the rat primary visual cortex. Activation of the nucleus basalis was shown to improve visual representations, by markedly increasing the encoding reliability of neuronal responses and by strongly de-correlating firing between cortical neurons. As attention has also been shown to increase reliability of neuronal encoding, by enhancing firing rate while reducing response variance,⁴⁸ and to cause a significant de-correlation of neuronal activity at the population level,^{49,50} the combined evidence may be consistent with the existence of a direct link between selective attention and cholinergic mechanisms. Additional work is needed to firmly establish this link.

THE ROLE OF COHERENT FIRING

Mounting evidence is showing that attention to a RF location may entail not only elevated baseline firing (see Section Top-down Control: Biases and Baseline Shifts) and enhanced responses to a stimulus occurring at the same location, but also increased synchronization of firing among the relevant neurons.⁵⁵⁻⁶⁰ Increased synchronization may or may not take the form of oscillatory patterns, but typically it does. Therefore empirical data is rapidly accruing to indicate that when attention is directed to a given location in the visual field, neurons with RFs encompassing that location will entertain in enhanced coherent firing, usually in the gamma-band frequency range, roughly from 30 to 70 Hz.61,62 In turn, increased synchronization of firing at the attended location may enhance synaptic transmission downstream of the considered neural population, effectively amplifying transmission of information in a spatially selective manner.⁵⁸ Analogous effects have been shown when attention is guided by feature information, rather than spatial information (see Section Feature-based Attention), with boosted synchronization of firing among the relevantly tuned neurons across the visual field.^{56,61}

Even though a reliable gamma-band effect can be observed in the near absence of consistent changes in the magnitude of single-neuron responses as a function of spatial attention,⁵⁵ most studies seem to suggest that the two types of effect usually coexist.⁵⁸ It is not excluded, however, that specific task parameters may lead preferentially to one or the other effect.

A fundamental question about synchronous firing of neurons as a correlate of attention concerns the understanding of whether the increase in coherence originates from intrinsic patterns of neuronal interaction within the visual cortex or whether it primarily results from inputs coming from other areas in the brain. Interestingly, a recent report has suggested a key role of the frontal eye field (FEF) in the initiation of an oscillatory coupling in the gamma-band frequency domain between local neuronal activity and activity in area V4.⁵⁹ This finding clearly suggests a key role of the FEF as a source of top-down signals affecting attentional processing in the ventral stream, a role that will be addressed further in a later section.

Attention-dependent modulation of neuronal synchronization has recently been demonstrated also for frequency domains outside the gamma range. For example, some studies reported a significant reduction in low-frequency oscillatory activity as an effect of spatially directed attention.^{55,58,59} Furthermore, it has been proposed that decreased synchronization in the low-frequency domain (delta-band, 1–4 Hz) may

reflect attention-related reductions in spontaneous low-frequency correlated rate fluctuations,⁵⁰ which effectively results in de-correlation of response variability among neurons in the population, with the ultimate consequence of increasing the signal-to-noise ratio in the pooled neuronal signal.

As delta-band oscillations are commonly associated to deep-sleep states and to compromised brain function, attention-related decrease in deltaband synchronization seems an obvious mechanism to ensure active and efficient processing. Contrary to this notion, however, enhancement of lowfrequency oscillations due to attention has also been reported,⁶³ leading to the hypothesis that delta-band synchrony can in some instances underlie efficient sensory-perceptual processing, especially when the task at hand in itself contains a matching temporal structure.⁶²

COMPETITIVE INTERACTION AMONG VISUAL STIMULI

A special problem for perceptual and attentional mechanisms to solve is one in which multiple stimuli are presented together, especially near to one another (crowding), and an individual must select the relevant stimulus while at the same time discarding any potential distracter. In neurophysiological terms, this translates into conditions in which multiple stimuli impinge simultaneously onto the RF of an individual neuron, including its surround, and they compete for controlling the neuron's firing pattern. It has been demonstrated that neurons along the ventral pathway, notably neurons in area V4 and the IT cortex, produce responses to two or more stimuli falling inside their RF that approximate the average of the responses elicited by the component stimuli presented in isolation.^{64–69} In other words, neurons in areas of the ventral pathway seem to be incapable of clutter invariance, a property that, if present, would allow them to encode the single most preferred stimulus inside the RF while automatically discarding other nearby stimuli, effectively implementing a MAX operation (in this case, the response of the neuron to multiple stimuli inside the RF would equal the response elicited by the single most preferred stimulus, that is the 'maximum' response elicited by each individual stimulus, and be completely unaffected by other sub-optimal stimuli). In contrast, it appears that multiple stimuli falling inside a single RF compete for the encoding capacity of the neuron, so that the neuron's firing is ambiguous as to which stimulus is encoded under these circumstances. It seems that competitive interactions among multiple RF stimuli

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are only weakly affected, if at all, by the specific nature of the stimuli involved, including the degree of their similarity (but see the discussion on luminance contrast in Section Top-down Versus Bottom-up in Selective Attention⁷⁰) except that the greatest competitive interactions occur with stimuli far apart in their ability to drive a neuron's visual response, like when a highly preferred and a null stimulus are involved.⁶⁹ Under these circumstances, the presence of the null or ineffective stimulus can drive the response to the preferred stimulus well below the level that the latter would have elicited if presented alone.⁶⁶⁻⁶⁹ An important notion that has emerged from these studies is that a stimulus which, on its own, causes only modest changes in firing rate when presented in isolation can nevertheless exert a profound (suppressive) influence on the neuronal firing when presented in combination with an effective stimulus, thus demonstrating clear-cut decoupling between effectiveness of stimuli in driving a response from the given neuron and their effectiveness in determining the firing rate of the same neuron. In terms of the latter property, an ineffective stimulus can be no less effective than a highly preferred, or optimal, stimulus in exerting control over the neuron's firing. In area V4, competitive interactions of this sort have been shown to span a limited extent of visual space, covering the RF size and extending only a small distance beyond the boundary of a neuron's RF.⁶⁷ In contrast, competitive interactions sometimes span a much larger extent of the visual field in IT cortex, including portions of the visual hemifield ipsilateral to the recorded hemisphere.⁶⁶ However, it has been reported that competitive interactions in IT cortex are much weaker, or nearly absent, when competing stimuli are placed across the vertical meridian,⁶⁶ as if competitive interactions could not come about at full strength when they involve the midline commissures (e.g., the corpus callosum). Selective attention mechanisms are needed to resolve these competitive interactions-the core notion of the Biased Competition Model of attention.²²

RESOLVING THE COMPETITION—SELECTION AND FILTERING

The Biased Competition Model of attention²² has been highly influential over the past 15 years, as it can account for a great deal of experimental observations obtained with a variety of approaches and techniques, both in human and animal studies of perception and attention. Mathematical and neural network implementations of the model have been

developed.^{68,71,72} The model rests on two tenets. First, as discussed in the previous section, multiple stimuli falling within the RF of a given neuron (and its surround) compete for controlling the neuron's firing rate. The most compelling evidence of this takes the form of suppressed responses to an effective stimulus falling inside the RF of a cell when it is paired with a second, ineffective stimulus for the cell, with responses to the pair approaching an average of the responses elicited by each of the two stimuli in isolation.^{64–69} Second, competition among stimuli can be resolved when a signal biases the competitive interaction in favor of either stimulus in the pair, thus causing the cell's firing to be primarily determined by the selected stimulus.^{29,35,66–68,70,73} When this occurs, selective attention is enacted: one of the competing stimuli is selected; the other is filtered out of the RF, or ignored. In cell physiological terms, a neuron's firing to multiple stimuli impinging on its RF (including its surround) as if only one of them were present corresponds to selecting a salient or otherwise relevant stimulus while discarding distracters.¹⁴

As already alluded to, competition between multiple stimuli can also take place between an effective stimulus impinging on the classical RF of the neuron and a stimulus (or stimuli) falling in the RF surround—a condition that is known to result in suppression of the visual response to the effective stimulus. Also in this case, attention can alter the competitive balance in favor of one or the other item, either filtering out the suppressive effect engendered by the surround stimulus or actually increasing it.⁷⁴ This immediately translates into the notion that attention can modulate center–surround interactions in visual cortex.

It should be realized that the set of phenomena accounted for by the Biased Competition Model can also be viewed as a particular instantiation of the Normalization Model of Attention (see Section Enhanced Processing of Attended Objects). Indeed, stimulation of a neuron with a pair of stimuli inside the RF, one effective and one ineffective, entails both a robust excitatory drive to the neuron due to the effective stimulus but also robust divisive normalization, as the ineffective stimulus will increase the strength of the suppressive drive pooled across the neuronal population. Under these conditions, the enhancement of the excitatory drive when attention is directed to the effective stimulus will restore its prominence in effectively controlling the activity of the neuron under study.⁴²

As already considered, the biasing signal for spatially directed attention may take the form of elevated baseline activity of the relevant neural population,²⁹ but the proposal has been made that increased synchronization of firing across the population of neurons with RFs encompassing the attended location may as well bias competition in favor of the relevant stimulus location.^{55,58} It remains to be established to what extent increased baseline firing and enhanced synchronization are related phenomena in functional terms. Regardless of this, likely sources of signals biasing competition in favor of the attended location include cortical areas such as FEF¹⁸ and LIP,⁷⁵ in the frontal and posterior parietal cortex, respectively, as well as subcortical structures, such as the superior colliculus.^{19,20} Future work might well reveal that other brain structures, at the cortical and subcortical level, also play an important role in controlling spatial attention.

Selection of a relevant object (or target) among competing stimuli can be achieved not only on the basis of its location in space, but also on the basis of its feature composition. For example, in visual search tasks, an observer is asked to find a target object among irrelevant distracters. Under some conditions, the target may be found easily, at no increasing cost as a function of the number of distracters, for example, when it is characterized by some unique property (known as 'pop-out'⁷⁶). In contrast, under less efficient conditions, locating the target may take some effort and increasing time as a function of the number of distracters.⁷⁷ Using search tasks of the latter kind, it has been shown that neurons in areas V4 and IT may contribute to the search process. In particular, as the search process unfolds, neurons in both areas come to encode the target but much less, or not at all, the distracters. Specifically, while neural activity shortly after search array onset to some extent represents all items in the array, later on, in anticipation of the behavioral response, only the target item activates the neural population which is selective for its constituent features, while neural populations activated by the features of the distracters are strongly suppressed. 56,66,67,73 This form of selective attention has been shown to engage similar underlying mechanisms to those engaged by spatially directed attention, except that here selection is guided by feature information. It has been further suggested that control signals for feature-based selection of a target object likely originate in at least partly different brain sources from those involved in delivering control signals for spatially selective attention. The proposal has been made that feature information specifying the target item and guiding its ultimate selection is represented within brain networks responsible for holding object feature information on-line during the execution of the task (working memory^{78,79}). In line with a notion of at least partial independence between space-based and feature-based control mechanisms, it has been claimed that spatial- and feature-based attention affect the activity of V4 neurons in a largely additive manner,⁸⁰ and the corresponding effects appear to develop with a distinguishable time course.⁸¹

Behavioral evidence obtained following lesion or deactivation of area V4 (and/or TEO) in the monkey is in full agreement with the Biased Competition Model of attention.⁸² This work has elegantly shown that, when selective attention mechanisms are knocked out by the lesion, the animal is at the mercy of stimulus salience. In other words, when multiple stimuli are presented and the animal must select a high-salience target among low-salience distracters, or when the target is shown in isolation, the animal performance is largely unimpaired. Conversely, when the animal is required to select a low-salience target among highsalience distracters, performance shows a dramatic drop. This can be explained by assuming that area V4 and TEO are key nodes within a network in which visual representations engendered by the retinal input compete for more central processes. It is known that competition can be controlled in bottom-up by the relative salience of concurrent stimuli,⁷⁰ the topic of the next section, whereas in the intact brain topdown control can overrule salience-based selection for the sake of current behavioral goals, this capability is instead severely compromised following damage to area V4 and/or TEO. This suggests that these areas, perhaps together with other brain structures, are essential to instantiate top-down mechanisms for stimulus selection, both in the macaque⁸² and human brain.⁸³ Evidently the above observation leads to the conclusion that salience-based selection can occur in visual areas that are still functional following damage to area V4 and TEO.

TOP-DOWN VERSUS BOTTOM-UP IN SELECTIVE ATTENTION

There is now evidence at the single-cell level that competitive interactions among multiple stimuli falling inside the RF of an individual V4 neuron are directly modulated by stimulus salience, such as can be obtained by varying the relative luminance contrast of the stimuli.⁷⁰ As already noted, with attention directed well outside the RF of the recorded neuron (e.g., to the opposite visual hemifield), adding an ineffective stimulus reduces responses of V4 (and IT) neurons to a concurrently presented effective stimulus for the neuron.^{64–69} It has also been shown that the suppressive effect is progressively stronger as

the contrast of the ineffective stimulus is increased, with the contrast of the effective stimulus held constant at an intermediate level (40%⁷⁰). Although the suppressive effect increases with contrast of the ineffective stimulus, notice that at the same time the ineffective stimulus presented alone may elicit a progressively larger, albeit weak, visual response when its contrast is increased.⁷⁰ This again indicates a remarkable dissociation between the efficacy of a stimulus to drive a visual response from a neuron and efficacy of the same stimulus to control the neuron's firing. A stimulus that, for its feature composition, may be largely ineffective in driving a visual response from a given neuron can nonetheless be highly effective

be largely ineffective in driving a visual response from a given neuron can nonetheless be highly effective in determining the neuron's response, due to its salience, or strength, such as its high luminance contrast. Moreover, within the same experimental context, attention directed to the ineffective stimulus in the pair has been shown to further enhance the suppressive effect exerted by this stimulus to the point that attention to a high-contrast ineffective stimulus almost completely dominates the cell's firing, namely it almost completely silences the cell.⁷⁰ These findings indicate that competitive interactions are entertained automatically within visual cortex and that competition can be resolved in favor of a highsalience (e.g., high-contrast) stimulus in bottom-up, in the absence of top-down signals reflecting the current volitional control on selective attention.

FEATURE-BASED ATTENTION

As noted previously, selective attention can be directed toward a specific spatial location,² or it can be guided by feature information specifying the target-defining properties.^{56,66,67,84} Furthermore, behavioral evidence in humans indicates that feature-based attention can affect processing throughout the entire visual field, in a parallel fashion.^{85,86} Consistent with this, single-unit recordings from area V4 of the macaque have revealed the correlates of this form of non-spatial selection. It has been discovered that neuronal responses to any potential target in the visual field-that is, any element that shares one or more of the target-defining features, including the target itself-are enhanced as the search process progresses, long before the animal actually locates the designated target. In other words, this form of feature-based attention is able to 'highlight' all the objects in the visual array that are potentially relevant for the task at hand.^{56,84} Essentially, the mechanism allows privileged processing of these objects, while other objects are effectively filtered out in parallel across the visual array. Although findings of this kind have come in slightly different flavors in the literature, perhaps related to specific characteristics of the experimental protocols, all converge to indicate that among the entire population of neurons in area V4 activated by the array elements, the neurons firing at the highest rate will be those directly stimulated by a feature in the RF that matches the feature preference of the neurons (e.g., red), while the animal is searching for a target item defined by the same feature (e.g., red). Evidently, depending on the currently relevant features, a specific control signal can target the neuronal populations with RFs anywhere in the visual field that are selective for the corresponding features, with analogous results found along both the ventral and the dorsal pathway.^{56,66,67,84,86,87}

Interestingly, evidence from a very recent study⁸⁰ has elegantly shown that feature-based attention can also alter tuning properties of neurons in area V4. Neuronal responses were recorded while animals deployed both spatial- and feature-based attention within the context of a modified match-to-sample task and a free-viewing visual search task. Especially in the former task, it was found that spectral tuning of many neurons in the population tended to shift in the direction of the spectral properties of the sought target. The emerging pattern of neuronal modulation effectively implemented a matched filter mechanism, whereby neurons in area V4 can be dynamically tuned to optimize encoding of currently relevant information. This effect is reminiscent of the shift in the RF profile toward an attended location described in Section Enhanced Processing of Attended Objects.^{30,51} Finally, recent findings have also shown that feature-based attention acts not only by enhancing neuronal firing but also by increasing synchronization among the neurons selective for the relevant features, particularly in the gamma-band frequency range.^{56,61}

OBJECT-BASED ATTENTION

It has long been known that attention mechanisms can not only operate on regions of space,² focusing processing on items at the attended location, but also on whole object representations. For example, observers are able to select and identify the multiple features of a target object while at the same time disregarding a spatially overlapping distracter.⁸⁸

A second implication of object-based attention mechanisms is that selection of some component feature of a selected object is naturally accompanied by processing of other features of the same object—a phenomenon termed 'cross-feature attention',⁸⁹ even when those other features are completely irrelevant for the task at hand.^{90–92} Therefore, it is easier to divide attention between different features of the same object than between features belonging to different objects.^{88,93–95}

Yet another consequence of this form of attention is that when attention is deployed to a specific point in space, enhanced processing is more likely to spread within the boundaries of an object encompassing the selected point, rather than across such boundaries.^{96,97}

Object-based mechanisms have been explored with a variety of methods including electrophysiological studies in the macaque brain.⁹⁸ A pioneering study of area V1 in the macaque investigated the neuronal correlates of object-based attention by using a curvetracing task.⁹⁹ The animal was required to make a saccade to one of two spots which was connected to the fixation point by a target curve, while ignoring a distracter curve. Multiunit neuronal responses for a given segment of a curve were compared across conditions in which the segment belonged to the target curve or to the distracter curve, which revealed enhanced neuronal responses elicited under the former condition.⁹⁹ This enhancement gradually spread from the fixation point to all portions of the target object while excluding the distracting object, even when the two curves crossed each other.¹⁰⁰ Interestingly, a subsequent study demonstrated a very strong correlation between neuronal activity in area V1 and behavioral performance of the monkey on each trial namely, saccades directed to the wrong end point were associated with enhanced neuronal response to the distracter curve passed a point of cross-over between the two curves.¹⁰¹ It remains to be investigated whether the observed neural correlates of object-based attention in area V1 depend on feedback from higher-order areas in the visual hierarchy.¹⁰²

Object-based attention can also be investigated within the framework of the Biased Competition Model (see Section Resolving the Competition—Selection and Filtering). As previously assessed for spatially separated stimuli impinging on the RF of a neuron,⁶⁹ a recent study¹⁰³ demonstrated that two superimposed objects elicit competitive interactions, which can be resolved either by top-down influences¹⁰⁴ or by exogenous factors.¹⁰⁵⁻¹⁰⁷ Specifically, single-cell recordings were obtained in visual area V4 while the monkeys were presented with two virtual surfaces overlapping in space, which were defined by patterns of dots rigidly rotating in opposite directions.¹⁰³ One surface was of the preferred color for the given neuron, whereas the other was of an excitatory equiluminant non-preferred color. In line with the well-known notion that abrupt onset of a stimulus automatically captures attention,²⁵ onset of one of the two surfaces was systematically

delayed and, as predicted, competitive interactions were resolved in favor of the corresponding surface. Significantly, neuronal responses to identical stimulus pairs were enhanced when onset of the effective surface was delayed as compared to when onset of the ineffective surface was delayed. The collected evidence therefore points to a role for area V4 in the implementation of object-based attention, although the contribution of other areas should not be excluded.

FEATURE-SELECTIVE ATTENTION

Unlike the form of feature-based attention discussed in a previous section, feature-selective attention is engaged under task conditions in which an individual is asked to identify, or otherwise respond to, a specific object feature while at the same time ignoring other features of the same object.¹⁰⁸⁻¹¹⁰ This form of attention, therefore, crucially entails that the unity of perceptual objects be broken down in order to cope with the current task due to the intervention of a mechanism that is directed at the level of feature dimensions. Feature-selective attention plays an important role in many real-life situations, for instance, when an individual must sort, or classify, objects on the basis of one elemental feature (e.g., color) while other features should be disregarded (e.g., shape and texture) [Figure 1(a)]. In addition, this type of feature-selective processing is tapped by a number of classical neuropsychological tests, such as the Stroop test¹¹¹ and the Wisconsin-card-sorting test.¹¹² In both cases, performance must be guided by selective feature information and interference from the irrelevant feature, or features, must be blocked or minimized.

The neuronal underpinnings of the latter form of feature-selective attention have been systematically explored in a recent single-unit recording study in which the activity of V4 neurons was recorded while animals were attending to either one or the other feature dimension of the task-relevant stimulus.¹¹⁰ Stimuli consisted of colored oriented bars. Two colors and two orientations were mapped onto one motor response (turning a response lever to the left), whereas two other colors and orientations were mapped onto the opposite motor response (turning the lever to the right). On half the trials, the color and orientation of the stimulus coded mutually exclusive behavioral responses. Therefore, in order to perform the task correctly, the monkeys had to selectively attend to the feature dimension that was cued as task relevant, while ignoring the other feature.

It was found that, under these task conditions, responses of V4 neurons to otherwise identical

FIGURE 1 | Sorting visual objects on the basis of feature information. (a) Any given sample of heterogeneous visual objects, such as sets of apples and sweet peppers in the present example, can be sorted, or classified, on the basis of any of their component features. For instance, they can be sorted on the basis of color information, while disregarding shape (type) information, as shown in the panels on top-left and bottom-right, or they can be sorted on the basis of shape (type) information, while disregarding color information, as shown in the panels on top-right and bottom-left. Therefore, actual sorting behavior must be guided by one or the other feature of the stimuli, depending on the currently relevant feature dimension. Disturbing influence from the competing feature dimension must be blocked in order to minimize potential for response conflict interference.^{108,109} (b) Example of neuron showing modulation of responses to a set of colored oriented bar stimuli depending on the currently relevant feature dimension. Crucially, the neuron tends to produce similar levels of firing to all selected features requiring the same behavioral response (see text for further details). Panel a, courtesy of G. Bertini and M. Veronese. (Panel b: reprinted with permission from Ref 110. Copyright 2007 Cell Press.)

stimuli were modulated depending on the component feature of the stimulus being currently attended. Most importantly, it turned out that a large fraction of the recorded neurons were able to 'cluster' the attended features of the stimuli into one or the other of two behaviorally relevant response categories, indicating that area V4 may be important in the process of converting selected feature information into a neural code available to guide the animal's behavioral responses.¹¹⁰ Specifically, in anticipation of the motor response, many V4 neurons exhibited similar activity for all feature values requiring the same motor output [Figure 1(b)]. Therefore, instead of encoding the selected feature of the stimulus as such, these V4 neurons encoded the behavioral response associated to the selected feature. Thus, in addition to examining a distinct form of feature-based attention, this work provides the first evidence that activity in area V4, until now thought to be a purely sensory area, encodes a behavioral response, albeit in a format



that is not motor in nature, but rather perceptually categorical.¹¹⁰

TOP-DOWN CONTROL: BIASES AND BASELINE SHIFTS

Given the distinction between attentional effects in sensory processing areas and control signals, researchers have sought direct evidence of control signals that may cause the attentional effects summarized previously. A key feature of these signals is that they ought to precede onset of task-relevant stimuli, that is, they should be present while the animal is attending to a given visual field location in preparation for performing a task on some relevant item. In practice, people have compared baseline activity of the neurons during the waiting period of the task between conditions in which the animal's attention was directed toward the RF of the studied neuron versus when attention was directed toward some location outside the RF. Single-unit recording studies have shown that neurons in area V4 (and V2) display elevated baseline firing during waiting periods while the animal is attending to a location inside the RF of the neuron in anticipation of RF stimulus onset.²⁹ It is interesting that analogous changes in baseline activity depending on the direction of spatial attention can be observed even when one compares attention to different locations inside the single RF, provided that the locations to be compared are not equally sensitive. Specifically, baseline activity has been shown to co-vary with the strength of the visually evoked responses at any given location within the RF.²⁹ Increases in baseline activity are typically small in absolute terms, in the order of a few spikes per second. However, in fractional terms, they can amount to a 50% increase in firing rate in the absence of visual stimulation.²⁹ Therefore, they represent a substantial percentage increment in neural activity over a relatively large population of neurons, those neurons with RFs encompassing the attended location.

The accepted account of elevated baseline activity due to spatial attention is that it reflects the influence of an incoming signal, originating from areas of the brain exerting control for spatially directed attention. In the case of area V4, these likely include areas in the posterior parietal and prefrontal cortices, 18,21,75 although subcortical sources (e.g., the superior colliculus^{19,20}) have also been implicated. Recent evidence obtained with low-current electrical microstimulation has directly demonstrated that signals of this sort originate at the level of the FEF, and they are capable of enhancing visual responses within area V4 at selected visual field locations.^{21,113,114} The same type of microstimulation was previously shown to improve the animal's performance in a demanding stimulus detection task.¹¹⁵ By contrast, muscimol inactivation of the FEF^{116,117} or of area LIP¹¹⁸ has been reported to produce spatially selective attention deficits within the context of a covert visual search task.

Spatially specific improvements in behavioral performance have also been obtained with lowcurrent electrical microstimulation of the superior colliculus,^{19,20} although it remains to be established whether microstimulation of the superior colliculus also enhances neuronal responses in area V4, and other areas along the ventral visual pathway. In summary, the available data suggest that a number of cortical and subcortical regions are involved in delivering control signals for spatially directed attention, and they largely overlap with critical nodes of the circuit controlling saccadic eye movements. These signals are likely responsible for elevated baseline firing in areas along the ventral pathway when attention is directed to a location inside the RF of the recorded neuron. The elevated baseline firing, in turn, may be part of the mechanism that confers to the targeted neurons increased sensitivity to visual stimulation. In addition, the same signals likely play a crucial role in boosting coherent firing of neuronal populations, a point that we have already made.

CONCLUSION

Research over the past 30 years has allowed impressive progress in the understanding of the brain mechanisms underlying the ability to concentrate mental resources onto a single location or object at any given time-an essential component of the ability to implement goal-directed behavior. Fundamental pieces of evidence have come from neurophysiological investigations in the awake, behaving macaque monkey. Science is very close to a full understanding of what it means at the single-neuron and at the network level to pay selective attention to a specific location or object, or object feature, including the fine details of the circuitry that brings about attentional modulation of firing in visual cortical areas, as well as the source and nature of the signals that control the same circuitry, thus initiating attention-related phenomena at the neuronal and behavioral level. The investigation of the neuronal correlates of visual selective attention along the ventral pathway of cortical visual processing has been particularly successful at identifying specific ways in which mechanisms for selective attention are intertwined with perceptual mechanisms for feature analysis and object recognition.

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