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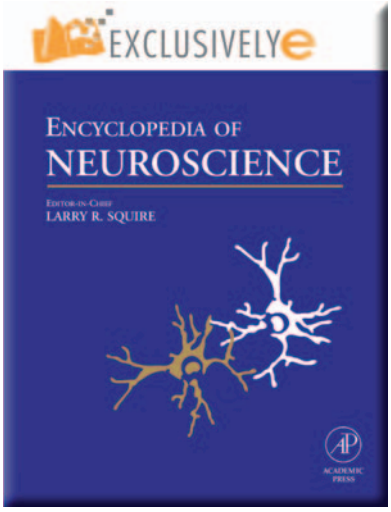

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Chelazzi L, Della Libera C and Santandrea E (2009) Attentional Mechanisms in Ventral Pathway. In: Squire LR (ed.) Encyclopedia of Neuroscience, volume 1, pp. 647-653. Oxford: Academic Press.

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Attentional Mechanisms in Ventral Pathway

L Chelazzi, C Della Libera, and E Santandrea,
University of Verona, Verona, Italy

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Introduction

Perhaps the most obvious form of visual selective attention is when individuals turn their gaze toward a salient or otherwise interesting object in their surroundings to align it with the high-resolution fovea of the retina. This allows more detailed processing of the fixated object at the expense 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 central processing due to selective attention.

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 selection of the next target for preferential, foveal analysis. In this vein, selective attention primarily assists the oculomotor system to optimize sensory sampling of the visual environment, given the current goal. Second, motor systems in general, including those for reaching and grasping movements, are physically constrained and can act only on one (or a few) objects at any given moment. Therefore, selective attention is needed to focus processing onto a single object in order to plan coherent behavioral responses targeted at the selected object. Third, 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 crowded environment. Therefore, selective attention is necessary to gate access of perceptual representations to memory systems. Finally, perceptual awareness is inherently limited in nature, and it unfolds serially, with a single perceptual representation gaining dominance at any instant in time. Therefore, selective attention is needed to allow entrance of the selected representation into working memory and conscious perception. On top of all the reasons above, students of vision and selective attention raise two further reasons why selective attention may be indispensable, and they are probably related. One reason is that processing of incoming retinal input must be focused on a single object at a time simply because, otherwise, processing and recognition of all objects simultaneously would overcome the limited processing capacity of the system. 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 all its elemental features, therefore preventing the erroneous binding of features belonging to separate objects in a cluttered scene. In brief, selective attention appears to be a key mechanism aiding efficient object recognition, perceptual awareness, goal-directed behavior, and selective memory storage.

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 two decades has been devoted to the investigation of the neuronal correlates of selective attention along the ventral pathway of cortical visual processing. 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 cortex, or area TEO, to culminate in a relatively vast cortical territory occupying the middle and anterior segments of the inferotemporal (IT) cortex. The ventral pathway represents a network of interconnected areas, largely organized according to a hierarchical scheme, whereby object representations are created with an ascending level of complexity and representational invariance. Ultimately, patterns of activity within IT cortex are now known to represent 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.

Studying the Manifestations versus the Control

In speaking of selective attention, one should distinguish between the manifestations and the causal control mechanisms. Specifically, one may use the term 'selective attention' to refer to the modulation of sensory processing along the ventral pathway in relation to concurrent changes in behavioral performance. In this case, the term would index the manifestations of visual selective attention at the neuronal, as well as at the behavioral, level. In contrast, one may use the term selective attention to refer to the signals that, within a given behavioral context, bring about the manifestations of attention considered above. The latter signals may or may not originate within the visual system, and the available evidence suggests that in most cases they do not. This article

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mainly concentrates on the manifestations of selective attention within the ventral pathway but also briefly discusses available evidence concerning the signals impinging on the ventral pathway to exert attentional control. Several forms of selective attention are distinguished, including enhanced processing of individual attended items, selective processing among competing items (or biased competition), feature-based guidance of target selection in visual search, and finally, feature-selective attention.

Enhanced Processing of Attended Objects: The Beneficial Effects of Spatially Directed Attention

Psychophysical studies of 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. In particular, attentional facilitation entails better detection of faint, low-contrast stimuli and improved discrimination of their features, as if attention to the stimulus led to enhancement of signal strength. 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. Consistent with these behavioral results, single-unit recording studies in the behaving macaque have found enhanced neuronal responses (e.g., in area V4) to a single stimulus presented inside the receptive field (RF) of the recorded 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. Overall, however, enhancement of neuronal responses to individual stimuli presented inside the RF is not very strong, typically on the order of 20%. Furthermore, the effect has not been found in all reported studies, and a possible account of this variability 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 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 at many stages of the visual system produce increasing responses as a function of stimulus contrast, up to a plateau, and the function takes the form of a sigmoid. 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. In line with this prediction, it was found that attention directed to an RF stimulus causes a leftward shift of the sigmoid relative to when the stimulus is unattended. As a consequence, responses to an attended stimulus will not differ reliably 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 of the neuron. These findings may explain, at least in part, why not all single-cell recording studies have found enhanced responses to attended compared with unattended single RF stimuli along the ventral pathway, including area V4, since 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 with stimuli at ignored locations. However, the effect is relatively large with stimuli of low contrast, whereas it tends to decrease with contrast of the stimulus.

Notice 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, whereas no detectable change in response latency is associated with manipulations of attention. This imposes some caution in likening effects of attention to changes in effective stimulus contrast.

An important question is whether directed attention, in addition to changing the strength of neuronal responses, will modify neuronal tuning for the stimulus features, for example, stimulus orientation. This has been addressed in a number of studies, and the prevailing view is that tuning properties of neurons are relatively immune to the influence of directed spatial attention, although they may be modified as a result of extensive discrimination training with perceptual learning protocols. Instead, spatially selective attention has been shown to cause a multiplicative scaling of tuning curves. Responses throughout the tuning curve will be multiplied by a constant factor, with no appreciable changes in the filter properties of neurons. Again, this is similar to the known effect on tuning curves of varying stimulus contrast. Nonetheless, it is conceivable that at the population

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level, a gain modulation of tuning curves allows finer encoding of features at an attended location than at an unattended one, for instance by reducing the signal-to-noise ratio at the attended location.

Top-Down Control: Biases and Baseline Shifts

Given the distinction between manifestations of attention in sensory processing areas and control signals, researchers have sought evidence for control signals that may cause the manifestations of attention 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 periods when the animal is attending to a location inside the RF of the neuron in anticipation of RF stimulus onset. 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 found to covary with the strength of the visually evoked responses at any given location within the RF. Increases in baseline activity are typically small in absolute terms, on 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. 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 in areas of the brain responsible for exerting control over spatially directed attention. In the case of area V4, these likely include areas in the posterior parietal and prefrontal cortices, although subcortical sources (e.g., the superior colliculus) have also been implicated. Recent evidence obtained with low-current electrical microstimulation has directly demonstrated that signals of this sort may originate at the level of the frontal eye fields, and they are capable of enhancing visual responses within area V4 at selected visual field representations. The same type of microstimulation was also shown to improve the animal's performance in a demanding stimulus detection task. Analogous effects on behavior have been obtained with electrical microstimulation of the superior colliculus, although it remains to be established whether microstimulation of the superior colliculus would also enhance neuronal responses in area V4 or other areas along the ventral 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 neurons increased sensitivity to visual stimulation.

Coherent Firing at the Population Level

Recent work has shown that attention to an RF location may entail, not only elevated baseline firing and enhanced responses to an RF stimulus, but also increased synchronization of firing among the relevant neurons. Increased synchronization may or may not take the form of oscillatory activity, but typically it does. Therefore evidence 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 an enhanced coherent firing, usually in the gamma-band frequency range, around 50 Hz. 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. It is interesting that this effect has also been observed under task conditions in which there was no consistent change in the magnitude of visual responses as a function of spatial attention. Therefore, enhanced processing and spike transmission at the attended location may take the form of increased firing, increased synchronization, or both. It remains to be established whether there are specific task parameters that lead preferentially to one or the other manifestation of attentional modulation.

Competitive Interactions among Multiple Visual Stimuli

A special problem for perceptual and attentional mechanisms to solve is one in which multiple stimuli

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are presented together (crowding) and an individual must select the relevant stimulus while at the same time discarding any potential distracter, in particular nearby distracters. In neurophysiological terms, this translates to conditions in which multiple stimuli impinge simultaneously onto the RF of an individual neuron and they compete for controlling the neuron's firing pattern. It has been demonstrated that neurons along the ventral pathway, including 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. In other words, neurons in areas of the ventral pathway seem to be incapable of clutter invariance, a property that, if present, would allow neurons to encode the single most preferred stimulus inside the RF while automatically discarding other nearby stimuli, effectively implementing a MAX operation. In contrast, it appears that multiple stimuli falling inside a single RF, or in its immediate surroundings, compete for the encoding capacity of the neuron, and the neuron's firing is ambiguous as to which stimulus is encoded. It seems that competitive interactions among multiple RF stimuli 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 of luminance contrast in the section titled 'Top-down versus bottom-up in selective attention'), except that the greatest competitive interactions occur with stimuli far apart in their ability to drive a neuron's visual response, as when a highly preferred or a null stimulus is involved. Under these circumstances, the presence of the null or ineffective stimulus can drive the response to the preferred stimulus well below the level that it would have elicited if presented alone. An important notion that has emerged from these studies is that a stimulus, which 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 activity. 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. 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. 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, 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.

Resolving the Competition: Selection and Filtering

The biased competition model of attention has been highly influential over the past decade, as it can account for a great deal of experimental observations obtained with a variety of approaches and techniques, in both human and animal studies of perception and attention. Mathematical and neural network implementations of the model have been developed. The model rests on two tenets. First, as discussed in the previous section, multiple stimuli falling within the RF of a given neuron (or in its immediate 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. 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 favored stimulus. 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 as if only one of them were present – the favored one – corresponds to selecting a salient or otherwise relevant stimulus while discarding distracters.

As already considered, the biasing signal for spatially directed attention may take the form of elevated baseline activity of the relevant neural population, 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. It remains to be established to what extent increased baseline firing and enhanced synchronization are related phenomena in functional terms. Regardless of this, we have already mentioned that likely sources of signals biasing competition in favor of the attended location include cortical areas

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such as the frontal eye field and lateral intraparietal area, in the frontal and posterior parietal cortex, respectively, as well as subcortical structures, such as the superior colliculus. Future work might well reveal that other parts of the brain, at the cortical and subcortical level, play as important a 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, such as when it is characterized by some unique property (known as 'pop-out'). In contrast, under less efficient conditions, locating the target may take some effort and increasing time as a function of the number of distracters. By means of search tasks of the latter kind, it has been shown that neurons in areas V4 and IT may contribute significantly 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. This form of selective attention has been shown to engage underlying mechanisms similar 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 regions 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 online during the execution of the task (working memory).

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. This work has elegantly shown that, when selective attention mechanisms are knocked out, 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, behavior is largely unimpaired. Conversely, when the animal is required to select a low-salience target among high-salience distracters, performance shows a dramatic drop. Consistent with a key role of area V4 in the implementation of attention mechanisms, this deficit has been observed following lesion of area V4 in the macaque, as well as following damage to the homolog of area V4 in the human brain. These findings suggest that, when the mechanisms for cognitively mediated selection are compromised, such as can be obtained through damage to area V4 (and TEO), competitive mechanisms and selection are primarily controlled by the intrinsic salience of objects, the topic of the next section.

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 luminance contrast of the stimuli. 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. It has also been recently shown that the suppressive effect is progressively stronger as the luminance contrast of the ineffective stimulus is increased, with the contrast of the effective stimulus held constant at an intermediate level (40%). Although the suppressive effect increases with contrast of the ineffective stimulus, notice that at the same time, the ineffective stimulus presented alone elicits a progressively larger, albeit weak, visual response when its contrast is increased. 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 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. These findings indicate that competitive interactions are entertained automatically within visual cortex and that competition can be resolved in favor of a high-salience

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(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, or it can be guided by feature information specifying the target-defining properties. Furthermore, behavioral evidence in humans indicates that feature-based attention can affect processing throughout the entire visual field, in a parallel fashion. Consistent with this, single-unit recordings from area V4 of the macaque have revealed the correlates of this form of nonspatial 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. 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.

Gating-Feature Information, or Feature-Selective Attention

Unlike the form of feature-based attention discussed in the 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. This form of feature-selective attention, therefore, entails that the unity of perceptual objects be broken down in order to cope with the current task. Feature-selective attention plays an important role in many real-life situations, for instance when an individual wishes to sort, or classify, objects on the basis of one elemental feature (e.g., color) and other features (e.g., shape and texture) must be ignored. In addition, this type of feature-selective processing is tapped by a number of classical neuropsychological tests, such as the Stroop test and the Wisconsin card sort test. In both cases, performance must be guided by selective feature information, and interference from the irrelevant feature or features must be blocked. 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 an animal was attending to either one or the other feature of differently colored, oriented bars. It was found that, under these task conditions, responses of V4 neurons to otherwise identical stimuli are modulated depending on the component feature of the stimulus being currently attended. Most important, it turns out that a large fraction of the recorded neurons are 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 categorical code available to guide the animal's behavioral responses.

Conclusions

Research over the past 25 years has allowed impressive progress in the understanding of the brain mechanisms underlying the ability to concentrate mental resources on 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 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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See also: Attention and Eye Movements; Attention: Models; Attentional Networks; Attentional Networks in the Parietal Cortex; Attentional Functions in Learning and Memory; Decision-Making and Vision; Neglect Syndrome and the Spatial Attention Network; Psychophysics of Attention; Vision for Action and Perception; Visual Attention.

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