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Spatial attention, feature-based attention and saccades: Three sides of one coin?

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Abstract

The last three decades has seen a steady growth of neuroscience research aimed at understanding the functions and sources of top-down attentional modulation in the brain. This correlates with recognition that attention may be a necessary component of sensory systems to support natural behaviors in natural environments. Complexity and clutter are two of the most recognizable hallmarks of natural environments, which can simultaneously contain vitally important and completely irrelevant stimuli. Attention serves as an adaptive filter allowing each sensory modality preferential processing routes for important stimuli while suppressing responses to distracters, thus optimizing use of limited neural resources. In other words, “attention” is the family of mechanisms by which organisms are able to effectively and selectively allocate limited neural resources to achieve specific behavioral goals. This review provides some historical context for considering attentional frameworks and modern neurophysiological attention research, focusing on visual attention. A taxonomy of common attentional effects and neural mechanisms is provided, along with consideration of the specific relationship between attention and saccade planning. We examine the validity of premotor theories of attention, which posit that attention and saccade planning are one and the same. While there is strong evidence that attention and oculomotor planning are similar, with shared neural substrates, there is also evidence that these two functions are not synonymous. Finally, we examine neurophysiological explanations for dysfunction in Attention Deficit Hyperactivity Disorder (ADHD) and the hypothesis that social impairment in Autism Spectrum Disorders (ASD) is partially attributable to perturbations of attentional control circuitry.

Introduction

What is the relationship between attention and motor action? Efficient navigation of complex natural environments requires a high degree of behavioral flexibility. In natural environments, individuals are routinely faced with the problem of selecting one from many possible motor actions. The appropriate choice often depends on internal state or behavioral goals. The flexibility to choose different actions in the face of similar, or even identical, sensory input based on internal state differences is a necessary precondition for efficient behavior in any moderately complex or dynamic environment. For example, consider that foraging animals must adjust their preferences and search strategies to track changes in food availability. Consequently, the behavioral relevance of particular stimuli can change –

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stimuli ignored one day must be attended to the next. Many of the problems arising from environmental complexity can be ameliorated by efficient allocation of sensory resources in support of specific goals, *i.e.* top-down attentional modulation. Top-down attention allows individuals to adjust to complex environmental conditions in many ways, ranging from subtle changes in existing behaviors to acquisition of wholly new behaviors based on goal-driven filtering of sensory inputs.

Premotor theories of attention (1) have long held that attention and saccade planning are really the same thing; that is, attention to a spatial location is always associated with a plan to execute a saccade towards the attended location (1-2), or *vice versa*. Although there is substantial evidence supporting this idea, there are also recent conflicting reports (3-6). While premotor theories account for many properties associated with spatial attention, they fail to account for others and largely ignore non-spatial attention. Regardless of mechanism, modulation of sensory processing by behavioral state, either at the organismal or single neuron level is critical for navigating complex natural environments and perturbations of the attention control system result in profound behavioral deficits.

Attentional modulation has been described in all sensory modalities. However, to date its mechanisms have been most studied in the context of vision. This is in large part related to the experimental accessibility of the visual system for neurophysiological recording experiments in non-human primates and the relative ease with which visual psychophysical methods can be combined with neurophysiological methods to identify and characterize attentional-related brain circuits. However, there is also a historical component, with many of the earliest and best understood demonstrations and models of top-down attention first appearing in the literature of visual psychophysics. The remainder of this article focuses on vision, however, many, if not all, of the ideas discussed are generally applicable to other modalities.

Historical Perspectives

The earliest descriptions of voluntary selective attention found in the scientific literature date back more than a century to the introspective observations of the psychologist William James (7). Recent years have seen dramatic increases in research focused on elaborating the brain circuits underlying attention. Today interest in attention is not limited to psychologists, but also includes neuroscientists using human and animal models of cognition and a variety of experimental approaches, as well as clinicians who are seeing increasing numbers of patients with attention-related conditions like ASD and ADHD. New lines of research have provided key insights into the physiological bases of attention and improved our understanding of how perturbations of attentional control can impact normal behavior.

Recently there has been increased effort among neuroscientists to make use of naturalistic stimuli and behavioral tasks in the laboratory designed to mimic natural experience (8). This is a critical step in ensuring that extant models of sensory processing, derived largely from experiments using highly controlled artificial stimuli and tasks, function under natural conditions. This approach has led to growing recognition that natural environments are exceedingly complex and information laden, possibly to the extent that without selective attention, sensory processing under natural conditions could exceed the brain's computational capacity. In the case of natural vision, visually-guided natural behavior generates a continuous pattern of spectrally complex and temporally dynamic retinal input. Spectral complexity arises from the fractal properties of natural objects and surfaces (9), while temporal complexity arises from frequent (2-3 Hz) saccadic eye movements (10-11), self-motion and motion of objects in the visual field. Even the primate brain, with its enlarged visual system (12) is unlikely to engender sufficient computational capacity to fully

process every photon captured in the retinas. Selective attention is one of several strategies the visual system employs to manage this vast amount of information. At a functional level, top-down modulatory signaling guides and focuses incoming sensory signals, effectively attenuating, or even discarding, irrelevant stimuli, with the net result of reducing or limiting the total amount of information reaching sensory and association areas under natural conditions (13-14).

In 1967 Neisser (15) articulated the foundations of what was arguably to become one of the most influential models of visual attention. Neisser's dual-mechanism hypothesis was premised on a functional dichotomy between extracting low-level visual features, like color, luminance and orientation, that could be effortlessly extracted from a scene, and high-level features, like facial or object identify. He suggested that high-level feature extraction required selective attention, with attention being a limited resource deployable to one object at a time, thus requiring sequential application of attention to each object to perform high-level feature extraction in complex or cluttered scenes.

The dual-mechanism hypothesis, with its pre-attentive stage for simple tasks, and attentive stage for more complex tasks, was subsequently elaborated in a seminal study by Treisman and Gelade (16) which provided behavioral evidence of a dual-mechanism model. Observers searched for visual targets in arrays of distracters; during singleton search, targets and distracters differed along a single stimulus dimension (e.g., red target, green distracters), while during conjunction search targets and distracters differed along multiple dimensions (e.g., red-horizontal targets, green-horizontal and red-vertical distracters). Their critical finding was that during singleton search, the time to find the target was independent of the number of distracters, while during conjunction search, each additional distracter item increased the time to find the target. These results were consistent with the idea that singleton search was pre-attentive, occurring in parallel throughout the visual field, while conjunction search required serial application of focal attention, as predicted by Neisser's dual-mechanism model.

Treisman and Gelade's (16) "Feature Integration Theory" is often referred to as the "attentional spotlight model". The attentional spotlight corresponds to a spatially restricted zone of enhanced sensory processing within the larger visual field. Enhancement leads to behavioral hypersensitivity, detectable as decreased reaction times or increased accuracy. Because the spotlight has no physical substrate, it can traverse the visual field independent of eye movements, although Treisman and Gelade, as well as studies from other laboratories (17-18) demonstrated a fixed switching time associated with moving the spotlight, effectively limiting the speed at which the spotlight could traverse a cluttered visual field.

Around the same time an equally influential paper by Posner (19) appeared relating psychophysically observed covert shifts of spatial attention to (then) new literature on the neural substrates of oculomotor planning based on recordings from midbrain and cortical neurons in awake behaving monkeys (20-21). Posner observed striking functional similarities between saccadic eye movements and covert shifts of spatial attention driven by endogenous and exogenous cues. These observations also seemed to support the idea of an attentional locus free to move about the visual field independent of eye position. The spatial cueing paradigms used by Posner and his colleagues were also readily adaptable for use with monkeys in conjunction with single neuron recording methods. The Posner cueing paradigm, in which observers maintain gaze on a central fixation target while covertly attending and responding to peripheral stimuli, has become the implicit basis for virtually all modern research on spatial attention in non-human primates (see Figure 1A).

A major factor leading to the long-lasting impact of both Treisman's Feature Integration Theory and Posner's concepts about covert attention is that both models articulated readily testable predictions about behavioral, and later neural, performance under a wide range of experimental conditions. These predictions were readily adapted for testing in non-human primates using modified versions of Posner's original cueing paradigm.

Neurophysiological correlates of spatial attention

In 1985, Moran and Desimone (22) reported that the activity of neurons in extrastriate cortex (area V4) of monkeys could be modulated by spatial attention. They found responses of V4 neurons to repeated presentations of identical retinal stimuli were dependent on where in the visual field the animal was attending (see Figure 1B). This seminal result suggested that V4 neurons acted like selective filters transmitting or blocking sensory information depending on the spatial relationship between their receptive field (RF) and the location of the attentional spotlight. This finding was confirmed in other laboratories (23-25) and similar effects were subsequently reported in both the dorsal processing stream (26-27) and primary visual cortex (28-29). Desimone and colleagues (see (30) for review) proposed the neural substrate for this effect was competition between cells or subunits representing the individual stimuli, with attention providing an activity bias to attended inputs, thereby increasing the chance that attended stimuli would win the competition and capture control of the neuron's output.

In most cases the experimental design of these studies closely follows the original Posner cueing paradigm (although see (28)): animals maintained central fixation while responding to peripheral cues, while spatial attention was directed towards particular locations using exogenous cues or instruction trials at the start of each block of trials. To a first approximation, there is a consistent and simple finding across these studies, independent of brain region: in a subset of neurons responses to attended stimuli are enhanced (i.e., fire more action potentials to the same stimulus).

Exactly what constitutes enhancement and the neural substrate of enhancement remain matters of debate (30-33). However, it seems that that most neural-level models of attention are consistent with the idea that attention increases the effective sensitivity of the neuronal population within the attentional locus either by increasing the amount of information these neurons transmit (29, 34) or by altering their contrast response functions (35-36). Neuronal sensitivity is usually well fit by a monotonically increasing sigmoidal contrast response function, which describes a cell's response (in spikes/sec) as a function of stimulus contrast. The lower the contrast level at which the sigmoid first significantly deviates from spontaneous background activity, the more sensitive the neuron. Changes in the horizontal position, overall gain or slope of the response function can all affect neuronal (and presumably behavioral) sensitivity. For example, either a leftward shift or a positive multiplicative scaling of the response function would reduce the minimum contrast at a neuron can robustly detect a stimulus (assuming attention doesn't affect spontaneous activity levels). To reiterate, although there is general agreement that the end product of spatial attention, at least in extrastriate areas, is a net increase in the sensitivity of neurons inside the attended region, whether this change is due to shifting, scaling or some other operation on the neuronal input-output function has yet to be determined (see (35-36); also see (37) for evidence of non-uniform modulation of selectivity and contrast-response).

A substantially different effect of spatial attention was reported by Connor and colleagues (38-39), who demonstrated that in V4 attention directed towards regions flanking the RF could shift the center of the RF towards the attended location. Attention-mediated RF shifts could improve behavioral sensitivity by increasing the number of neurons representing the

attended region, effectively increasing the signal-to-noise ratio for target detection. Womelsdorf *et al.* (40) recently obtained similar results in area MT, demonstrating that RF shifts are not unique to the ventral stream. There is also computational support for shifting RFs (41) and shift-like effects on feature-selectivity have also been reported in the domain of feature-based attention (42-43). Interesting, Compte and Wang's (41) computational model demonstrated that simple changes in neuronal sensitivity at an earlier stage of processing could be the underlying mechanism for shifting RFs, suggesting a possible a common substrate for attentional effects.

Neurophysiological correlates of feature-based attention

Until recently, neurophysiological studies have focused almost exclusively on spatial attention, (although see (44-46) for important exceptions and (47) for a review for feature-based attention). Studies of spatial attention seek to answer a question raised by the original spatial cueing experiments: what are the neural mechanisms responsible for observer hypersensitivity to stimuli at attended locations?

Visual attention, however, is clearly *not* restricted to the spatial domain (14, 48). Cues can equally well indicate target features, like color, orientation or texture. Innumerable psychophysical studies have demonstrated that cues informative about the visual appearance of a target (without providing information about the target's spatial location) also result in enhanced target sensitivity (18, 49). Many biologically inspired models of human vision that function particularly well under naturalistic conditions incorporate distinct spatial and feature-based attentional modules (18, 50). Wolfe and Horowitz (14) argued that color, motion, orientation and size perception are subject to attentional modulation and identify an additional 15 stimulus properties likely to be attentionally modulated.

Despite the clear behavioral significance of feature-based attention, namely the importance of being able to attend to behaviorally relevant items based on appearance, instead of location, we know relatively little about its neural substrates. However, several studies have demonstrated robust neural correlates of feature-based attention. Treue and Martinez-Trujillo (46) demonstrated the visual responses of direction selective neurons in parietal area MT were modulated depending on whether monkeys were detecting motion in the neuron's preferred or non-preferred direction. This experimental finding is the basis for the "feature-similarity gain" model (46, 51), which proposed that feature-based attention could be modeled by a variable neuronal gain term proportional to the similarity between the target and a neuron's preferred stimulus, i.e. if the target resembles the preferred stimulus, gain is high and the neuron is very sensitive, conversely, when the target does not resemble the preferred stimulus, gain is low, resulting in baseline, or even reduced, sensitivity. Overall this makes the whole visual system more sensitive to target-like features.

This resembles the effects of spatial attention described above, where attention acts to increase the gain of neurons with RFs inside the attended region. In the case of feature-based attention, attention acts to increase the gain of neurons with visual selectivity profiles that include features present in the target. In both cases, gain changes are proportional to the correlation between the attended target's properties (location or appearance) and a neuron's visual selectivity profile (either spatial or feature).

Similar feature-based attention effects have been described in area V4 using naturalistic stimuli (43). However, in V4 the specific rules relating the visual appearance of a target to observed changes in neuronal selectivity are not yet fully understood. Nonetheless, the most common effect of feature-based attention in V4 appears to be multiplicative gain changes similar to those observed in MT (43).

Reminiscent of Connor *et al.*'s (38-39) finding of RF shifts driven by spatial attention, David and colleagues (43) reported that in a subset of V4 neurons feature-based induced shifts of orientation and/or spatial frequency tuning profiles depending on the spectral properties of the target, suggesting the basic mechanisms – gain modulation and tuning shifts – are conserved for both spatial and feature-based attention.

Origins of the top-down signal?

A key, yet unresolved, question concerns the origins of top-down modulatory signals. In the laboratory attentional effects can be engaged by a variety of experimental manipulations. The classic example is the Posner paradigm illustrated in Figure 1A, however, spatial working memory can also instantiate attentional effects (5, 52). Given the long held belief that prefrontal cortex (PFC) plays a critical role in establishing and maintaining working memory (53), it is not unreasonable to assume that PFC is the ultimate source of attentional modulation. At this time, however, current work has only gone as far as identifying the frontal eye fields (FEF) as a likely proximal source of modulation in early visual areas. A series of elegant studies by Moore and colleagues provide strong evidence in support of this conjecture. Moore and Fallah (54) demonstrated that localized, sub-threshold (i.e., insufficient to elicit eye movements) electrical microstimulation in the FEF increased behavioral sensitivity at the visual field location corresponding stimulation site, showing FEF activation could mimic the behavioral effects of spatial attention. Armstrong and colleagues (55-56) recorded from matching sites in the FEF and V4 and found that FEF microstimulation could also mimic the physiological effects of attention in V4 neurons.

Implications for premotor theory?

As noted above, there are unmistakable similarities between spatial attention and saccade planning. The fact that activation can both drive eye movements and mimic the effects of covert attention (54-56) supports the contentions of premotor theory. However, it is possible that these similarities are superficial and not indicative of a common neural substrate. For example, gaze can be directed toward only one location in space. When the premotor theory first appeared in the late 1980s, it was generally believed that the same was true of spatial attention. However, recent studies have provided both psychophysical (3-4) and physiological (57-58) evidence that spatial attention can be simultaneously allocated to multiple non-contiguous regions of the visual field.

Perhaps the most recent compelling evidence in support of a common circuit for saccade planning is Hoffman and Subramaniam's (2) finding of enhanced visual processing at saccade endpoints, which they argued demonstrated the impossibility of planning a saccade to one location while maintaining attention at another, consistent with a common neural substrate. However, there are counter examples. Golomb and colleagues (5) demonstrated that with an appropriately designed task subjects could plan and execute saccades while simultaneously remembering and attending to a cued location. Juan and colleagues (59) demonstrated a dissociation between attention and saccade planning in non-human primates.

This is not to say that oculomotor planning and spatial attention do not share neural substrates. There is ample neurophysiological and neuroanatomical evidence that cortical regions, like the FEF and the lateral intraparietal area (LIP), as well as sub-cortical structures like the superior colliculus (SC), are critical for both saccade planning and attentional allocation (see (60) for complete review). However, in many cases, it remains unclear whether these areas are comprised of homogenous neuronal populations participating in both eye movements and attention, or a heterogeneous population, with some neurons driving oculomotor behavior and others driving spatial attention.

Another issue is the fact that premotor theories account only for spatial attention effects. There are little or no mechanistic similarities between saccade planning and feature-based attention, other than (1) many of the brain regions implicated in both saccade planning and spatial attention, like FEF, LIP, V4 and the SC, also exhibit feature-based attentional modulation and (2) feature-based attention, which can be used to select targets based on visual appearance, is likely to contribute in some way to saccadic target selection in cluttered environments (42, 61).

Spatial and feature-based attention share key common properties – the end result of both is enhanced sensitivity to attended features. Neurophysiological studies suggest that both can be modeled as changes in neuronal contrast response functions. Interestingly, the Reynolds and Heeger's recently published spatial attention model (35) turns out to be capable of modeling many feature-based attentional effects. At this point in time, it seems like a common neural substrate for spatial and feature-based attention would be difficult to reconcile with current premotor theories premised on the idea of a common substrate for saccade planning on spatial attention.

Attention Deficit Hyperactivity Disorder (ADHD) and dysfunction of the executive control system

Recent estimates suggest upwards of 5% of children worldwide are impacted by ADHD (62-64), the hallmarks of which include increased distractibility and inability to efficiently deploy attentional resources. The etiology of ADHD is not fully known and there are likely multiple contributing factors, including genetics (65-66). A number of studies have suggested that the symptoms of ADHD are linked to dysfunction of the catecholaminergic components of the executive control system (67), the prefrontal-based network that facilitates flexible, goal-driven behavior (53). This system is a potential (indirect) origin of the top-down signals modulating visual cortex (68-69). Consistent with this idea are recent quantitative studies demonstrating impaired spatial attention and cueing effects in individuals with ADHD (70-71). However, it should be noted that performance on spatial attention tasks could also be affected by increased impulsivity and some forms of ADHD (72) and various types of prefrontal dysfunction (53) are often associated with increased impulsivity. At this time relatively little is known about how ADHD affects top-down modulation of the sensory cortices; this question remains an important area for future research, particularly in animal models where neurophysiological methods can be applied.

Perturbations of the attentional system in Autism Spectrum Disorder (ASD)

Given the similarities between spatial attention and oculomotor planning it is interesting to note a recent series of studies comparing saccadic eye movements in autistic and non-autistic subjects that suggests some of the social impairments associated with ASD may be attributable to abnormal attentional processing. Klin and colleagues (73) recorded the eye movements of age- and IQ-matched autistic and control subjects viewing scenes from the 1967 film “Whose Afraid of Virginia Wolfe” containing intense social interaction. Analysis of eye movements revealed that autistic individuals spent significantly more time viewing the mouth, body and objects in each clip, compared to control subjects, who typically fixated on the actors' eyes. This finding is consistent with the social impairments associated with ASD; the eye movements and gaze direction provide important social signals, so it's not surprising that social control subjects preferentially view eyes. The mouth, body and objects, which preferentially drew the gaze of autistic subjects, exhibited more low level motion than the eyes. Since attention can be captured by highly salience low-level cues, e.g., a bright flash, loud noises or fast movements, and attentional capture is typically followed by saccades to the attended location. One interpretation of these data is that in control subjects

attentional capture by low level stimuli is effectively suppressed to enable tracking of the social interactions appearance on the computer screen. Autistic subjects, however, fail to suppress attentional capture resulting in vital attentional resources being deployed to track irrelevant low-level stimuli. Although this work is ongoing, these studies, along with a recent developmental study demonstrating impaired attentional capture by biological motion in ASD patients as young as two years of age (74), suggests that disruption of the attentional control system may be at least partially responsible for some of the distinctive behaviors and social impairments associated with ASD.

Conclusions

During natural vision, we are constantly barraged by overwhelming amounts of sensory stimulation. Making sense of natural stimuli and reliably initiating appropriate behavioral responses to correct environmental stimuli is a difficult problem; understanding this process is a critical step towards developing a complete model of sensory processing. Both spatial and feature-based attention can facilitate natural behavior by reducing a potentially overwhelming flood of sensory information down to manageable levels. At this time, we know considerably more about the neural substrates of spatial attention. However, recent studies have provided important insights into the mechanisms for feature-based attention as well. There is growing behavioral and neurophysiological evidence that spatial and feature-based attention share similar features, employ similar computational algorithms and perhaps even have a common neural substrate. In relation to saccade planning, premotor theory (1), strictly interpreted, suggests that saccade planning and covert spatial attention are one and the same. While there is substantial evidence that oculomotor planning and attention are functionally similar – studies using microstimulation and anatomical tracing techniques support the idea that top-down modulation in early visual cortex has origins in oculomotor areas, like the FEF (54-55). However, recent studies have also revealed subtle differences between saccade planning and attentional allocation that suggest these functions may share neural substrates, but are not one and the same (5-6, 75-76). Finally, recent work linking sustained working-memory and attention suggests that memory could be a critical link between or even a common source of modulation for spatial and feature-based attention (52). The behavioral consequences of attentional disruption are debilitating. In the future, neurophysiological explorations seeking to identify the low level neural substrates of top-down attentional signaling are likely to provide important insights into both the etiology and treatment of attention-related disorders.

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Figure 1.

Experimental paradigms for probing attention. (A) Covert spatial attention task (modeled after (19)). The observer fixates on the +. A transient, spatially localized visual stimulus cues the observer about where to attend. After a randomized delay, a probe stimulus appears at the cued location (“valid” trial, as shown) or an uncued location (“invalid” trial, not shown). The observer must make a speeded response indicating detection of the probe. In normal observers, reaction times on valid trials are shorter than invalid trials, all other variables held constant. (B) Schematic illustration of Moran and Desimone’s (22) original finding of attentional modulation in extrastriate visual cortex. Monkeys were trained to attend to a small region on a computer screen (indicated in red). Monkeys performed a match-to-sample task (while maintaining central fixation) that required covertly attending to the stimulus on either the left (upper panel) or right (lower panel) side of the neuronal receptive field (dashed line), while ignoring the other. The location of the attended region was varied in blocks. In both types of trial, the pattern of retinal stimulation was identical. Stimuli were selected to be either effective or non-effective at eliciting visual responses in the absence of attention. Bar chart on the right summarizes the key finding in V4: although the pattern of retinal stimulation in the attend “good” and “bad” configurations was identical, many V4 neurons responded as if the attended stimulus were presented in isolation, effectively filtering out the unattended stimulus.