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A Stage Theory of Attention and Action

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WE BELIEVE a wide range of empirical findings and theoretical views can be organized by the *stage theory of attention and action,* which holds that decisions to shift gaze to a particular location are almost entirely dependent upon two cognitive processes. The first is a selection process corresponding with the allocation of visual-spatial attention, and the second is a response process that produces movements of the eyes or other effectors. Importantly, though, attentional allocation and response preparation, although linked, are distinct process accomplished by different networks of neurons spanning multiple cortical and subcortical structures. By bringing into focus the sensory–motor transformations underlying flexible, visually guided behavior, this theory moves beyond the biased competition theory (that only addresses target selection and attention allocation) and the premotor theory of attention (that identifies target selection entirely with saccade preparation). The theory also provides a framework for understanding rapid error correction, flexible stimulus–response mapping, and the adjustment of processing speed relative to accuracy.

It is important for us to begin with two definitions to lay the groundwork upon which this theory is built. First, we will discuss how perceptual attention influences early visual processing. We believe that one of the most difficult aspects for both producers and consumers of attention research is adequately defining what is meant by the term "attention." This is a result of the use of the term attention to describe selection mechanisms that operate during a great variety of computations that the brain performs (Luck & Vecera, 2002), as well as to characterize certain kinds of neural modulation (Reynolds & Chelazzi, 2004) in senses that are not always compatible. Indeed, much of the literature on divided attention utilizes the psychological refractory period (PRP) paradigm, and there is abundant evidence that the observation of capacity limits in this paradigm is often due to a limit in our ability to select multiple responses at the same time (e.g., Pashler, 1994). For this reason, we will use the term "perceptual attention" to refer to those selection mechanism or mechanisms that focus processing on task-relevant inputs, such that internal representations of important incoming information can be built most efficiently (see Chapters 1 and 4 of this volume). This serves to disambiguate the topic of our discussion from other selection mechanisms and states of arousal that have fallen under this catchall term (e.g., selection for storage in working memory, response selection, dual-task performance, vigilance, etc.). Making this distinction is particularly important given existing evidence that different selection mechanisms can be dissociated (Thompson et al., 1996; Woodman & Luck, 2003a; Woodman, Vogel, & Luck, 2001a). Second, throughout the presentation of the stage theory of attention and action, we will describe the cognitive and neural activity that results in an overt response (e.g., the movements of the eyes or a manual button press) as a stage of cognitive processing (see Chapter 7 in this volume). At the extreme, this is controversial, given that the operations carried out by the brainstem could hardly be described as cognitively penetrable. However, our use of this term is built on the previous work that describes the operations of deciding to make a given movement and preparing that response as an operation under cognitive control (Logan & Cowan, 1984; Luce, 1986; Ratcliff, 2006). The justification for our usage of the terms "perceptual attention" and "response stage of cognitive processing" is a primary point of the stage theory and will developed throughout our discussion.

The stage theory of attention and action is derived from four propositions. First, the cognitive processing necessary to perform every task of interest to cognitive scientists is accomplished by dissociable processing stages. Although this is one of the oldest proposals in cognitive science, we will describe how modern neuroscientific evidence has validated and enlivened it. Second, the demands of a given task are met by transformations within specific stages (e.g., target selection and response preparation) and by transmission between stages (e.g., stimulus–response mapping, speed–accuracy adjustment). Third, the theoretical constructs of the onset of processing of a stage, the rate of information accumulation within a stage, and the threshold level that enacts decisions are realized in the patterns of activity of specific networks of neurons that account for the variability of response time (RT). Fourth, executive control that enables correction of errors that occur before visual processing is complete, flexible stimulus–response mapping, and speed–accuracy adjustments originates in a neural network distinct from those selecting targets and producing responses. We propose that this executive control interacts with the response preparation process but not with target selection, although other executive control mechanisms can and do guide this operation of perceptual attention.

EVIDENCE FOR DISTINCT FUNCTIONS AND STAGES

Cognitive psychology has shown that human RT data cannot be explained without allowing for the existence of successive stages of processing (Donders, 1868/1969; Luce, 1986; Sternberg, 2001) even in models that identify all the interesting variability in RT and response probability with a single stage (e.g., Ratcliff & Smith, 2004). Cognitive theories have proposed that these stages may overlap in time (McClelland, 1979) or be at least partially overlapping (Miller, 1988), but essentially all such large-scale models have this characteristic. Most of these cognitive models have the commonality of describing separate stages of perception and response processing, with some also discussing the subcomponents of perceptual processing (Treisman, 1969) and many ignoring the proposal of a similarly serial flow of information through memory stages (Atkinson & Shiffrin, 1968). Signal detection theory (Green & Swets, 1966) may seem to contradict this norm, being static in nature. However, like its complementary counterpart, biased choice theory (Luce, 1963), signal detection theory adds to its sensitivity metric a bias metric that allows for the subject's willingness to respond, which is set prior to the appearance of a stimulus.

The interpretation of event-related potential (ERP) recordings presents no clear alternative to a stage-like view of information processing in the human brain. That is, the ERPs time locked to the onset of a visual search array allow us to visualize the sequence of processing as cognition unfolds (see Figure 9.1). The series of ERP components indicate that information is transformed from the sensory components most sensitive to low-level visual features (i.e., the C1, P1, and N1 components), to waveforms modulated by the deployment of attention (e.g., the N2 posterior contralateral [N2pc]), followed by components associated with categorization of the visual stimulus (e.g., the N2/P3 complex), waveforms indexing working memory updating (i.e., the P3 and contralateral delay activity), then waveforms elicited by the preparation of the response (i.e., the lateralized-readiness potential or LRP), ending with waveforms elicited during the intertrial interval related to evaluating performance on the trial that just occurred (e.g., the error-related negativity or ERN). A detailed discussion of how findings from ERP experiments support the stage theory is beyond the scope of this chapter. Instead, we refer readers to more detailed accounts of the cognitive mechanisms indexed by ERP components (Luck, 2005; Rugg & Coles, 1995) and will focus on research that integrates findings from ERP recordings with another primary neuroscientific technique, single-unit recordings (see also Chapter 1 of this volume).

Neuroanatomical observations also invite—if not demand—the concept of stages of processing. Anyone who looks at a histological section of cerebral cortex must notice the morphological diversity of neurons arranged in different layers. Given the well-known relation of structure and function in nervous systems, this anatomical diversity predicts a corresponding physiological diversity. However, the range of neuron types described in areas like the frontal eye field (FEF) hardly matches the anatomical diversity. The literature hints at a large variety of neurons in the FEF (Bruce & Goldberg, 1985; Schall, 1991), but the history of neuroscience teaches that functional diversity is proportional to morphological diversity.[1] According to the logic of labeled lines, a distinction between neural processes must correspond to distinct functional processes. For example, distinct fibers originating in different

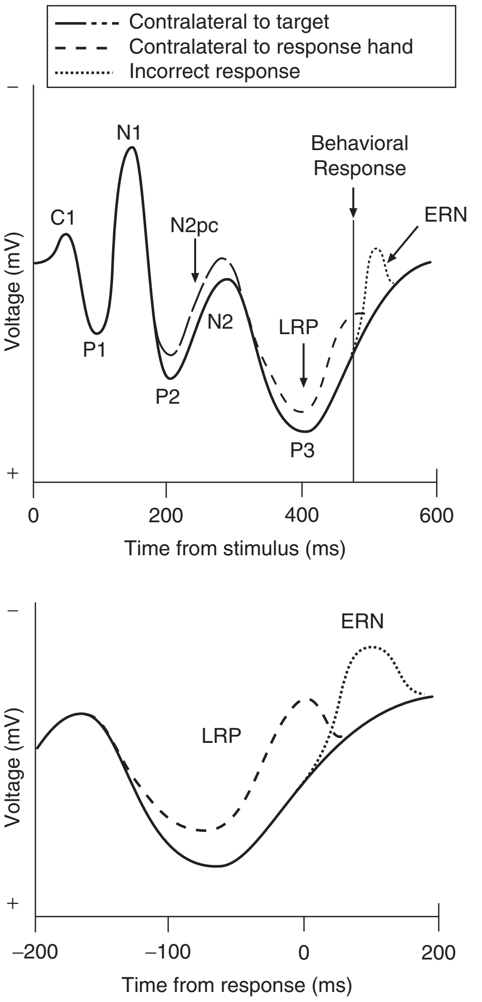

FIGURE 9.1 Idealized event-related potential (ERP) waveforms from humans elicited during a visual search task. Top panel shows the sequence of ERP components from the earliest sensory responses (i.e., the C1 component) to the performance monitoring responses (i.e., error-related negativity [ERN]). The ERP components are labeled using the conventional polarity-ordinal nomenclature. Bottom panel illustrates how ERP components time-locked to the response are related to response preparation and evaluation of task performance. Note that the lateralized components are not typically observed at the same electrode sites but are shown in the same waveform here for illustration purposes. Abbreviations: C1, Component 1; P1, 1st Positive component; N1, 1st Negative component; P2, 2nd Positive component; N2pc, 2nd Negative component; Posterior, Contralateral; N2, 2nd Negative component; LRP, Lateralized-Readiness Potential; P3, 3rd Positive component; ERN, Error-Related Negativity.

sensory receptors and terminating in different brain centers lead to distinct sensory experiences, like sight or touch. Likewise, if a neural representation of a stimulus that must be located and categorized to guide a saccade can be distinguished from a neural representation of the endpoint of a saccade, then this would be evidence for two functional kinds of selection. In fact, we have distinguished two types of visual selection neurons, one that selects the stimulus and the other that selects the endpoint of the saccade (Sato & Schall, 2003; Schall, 2004). The formulation of this theory also calls attention to obvious facts that are often not considered in functional descriptions. For example, in higher cortical areas, some neurons are anatomically closer to the retinal input whereas others are closer to the muscles. These afferent and efferent relationships are embodied by the specific distributions of cell bodies, dendrites, and afferent axon terminals in the different cortical layers. Each layer has different intrinsic and extrinsic connections, so the diversity of neurons is embedded in a diversity of circuits. Laminar differences in cell body and axon terminal location translate into differences in connectivity with excitatory and inhibitory neurons (e.g., Medalla et al., 2007) that have important functional implications. For example, local connections respect efferent targets (Vicente et al., 2008). Currently, the variety of functional hypotheses is at least an order of magnitude less than the variety of neurons distinguished by morphology, location, and connectivity. The mathematical and statistical elegance of sequential sampling models does not necessitate that a unique population of neurons instantiates each process directly. However, that is an intuitive assumption that simplifies the evaluation of such models using neuroscientific methods. On the other hand, the functions proposed by models (e.g., sequential sampling and race models) may be instantiated by a multiplicity of morphologically distinct neurons. Although, if the latter were the case, then specific linking propositions would be difficult to work out. Alternatively, the functional process models may require refinement into smaller functional parts.

Recording from the neurons in visuomotor structures like the FEF also allows little room for doubt that the brain has distinct networks of neurons performing different functions that span the sensory–motor continuum. As shown in Figure 9.2, the FEF includes a type of neuron that participates in selecting targets for orienting after an array of objects appears (visual neurons) and another type of neuron that contributes to preparing to execute (planning) saccadic eye movements (movement neurons). These types of neurons are clearly distinct in the functional roles they play (as will be elaborated below). They are also probably distinct in their laminar distribution (although definitive data remain to be gathered) and, thus, in their afferent and efferent connectivity. They are also heterogeneous, ranging between shorter or longer latencies of response, more transient or sustained, selecting the location of the attended object or the endpoint of the saccade. They are also not the only types of neurons in the FEF, for it also consists of neurons active specifically during fixation, others active specifically after saccades, and a commonly encountered type referred to as *visuomovement neurons*. The visuomovement neurons respond to visual stimuli, have maintained discharge rates even if the stimuli disappear and finally exhibit a pronounced increase of discharge rate before saccades are initiated. This intermediate type of neuron is often interpreted as both visual- and movement-related; however, we have recently obtained evidence that visuomovement neurons are biophysically distinct from visual and movement neurons (Cohen et al., 2009c) and that they are not modulated in a manner consistent with the function of preparing saccades (Ray et al., 2009). For the purposes of this chapter, we will focus our attention on those visual neurons that select targets for orienting and the movement neurons that lead to overt responses. Ultimately, because the FEF is a prefrontal area that receives converging inputs from a multitude of other cortical areas, we believe that it can be interpreted as a microcosm of the key processes necessary for accurate visually guided saccades.

THE STAGE THEORY OF ATTENTION AND ACTION IN ACTION

To present the theory, we describe the sequence of transformations and transmissions that occur

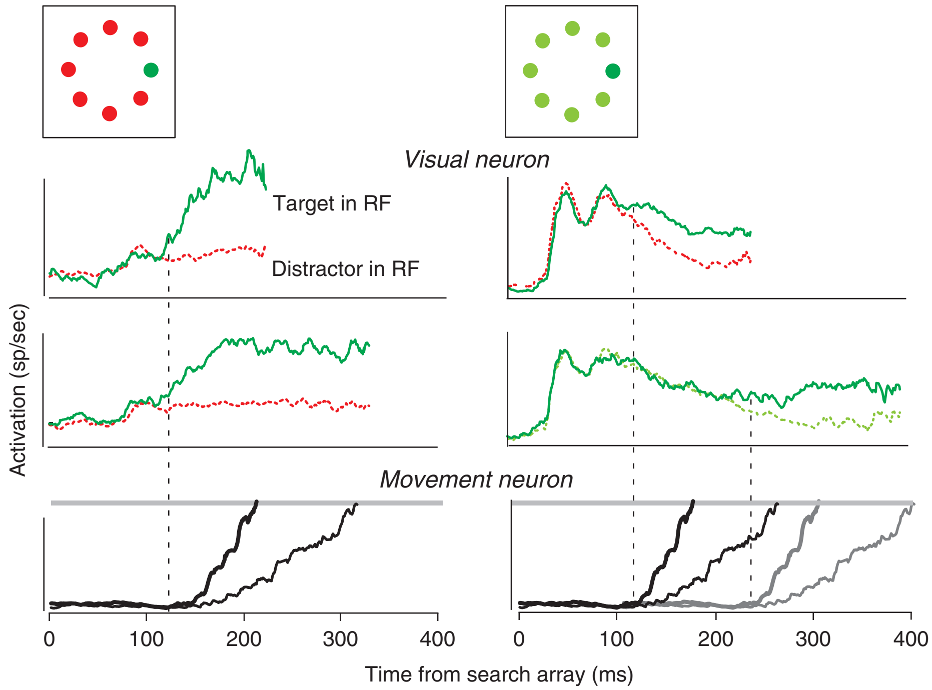

FIGURE 9.2 Two stages to direct a saccade during efficient (*left*) and inefficient (*right*) search for a color singleton recorded in the frontal eye field (FEF) of monkeys. Activity of two visual neurons (*top two panels, left and right*) and movement neuron (*bottom panels*) are illustrated. Visual neuron activity is shown for trials when the target appears in the receptive field (RF; *green*) and for trials when the distractor is easy to distinguish from the target (*red*) or the distractor is difficult to distinguish from the target (*light green*). During efficient search, visual neurons in the FEF select the target at a relatively constant interval after the array appears. Saccades are initiated when the activity of movement neurons reaches a threshold (*gray horizontal bar*). Saccades are initiated earlier (*thick*) or later (*thin*) according to variation in the rate of growth of the activity. The systematic delay of response time (RT) when search is not efficient comes about because the movement neurons do not begin accumulating activity (*gray plots on right*) until the target is selected by visual neurons, with variation in rate contributing additional variability in RT.

from visual stimulus encoding until extraocular muscle contraction in a participant performing a visual search task in which a target is embedded in a cluttered scene.

Task Set Preparation

Every trial of every task is embedded in history. Consequently, each trial begins in some state of preparatory set. For an observer who is sufficiently motivated, the outcome of the previous action can guide the participant to become more or less cautious, which will influence the ultimate RT through executive control (e.g., Rabbitt et al., 1979; Emeric et al., 2007). For example, when an observer performs a feature search task, the target is located effortlessly and is said to “pop-out.” However, when the target versus distractor features in the array switch between trials, then performance is slower and more error-prone (Maljkovic & Nakayama, 1994; Maljkovic & Nakayama, 2000) in a manner that can be attributed to neural processes in the FEF (Bichot & Schall, 2002). Also, visual search performance changes with longer-term experience with search arrays (e.g., Chun & Jiang, 1998; Bichot & Schall, 1999; Chun, 2000; Johnson et al., 2007).

Such adjustments based on trial history require some kind of memory. Although it is proposed that visual search tasks have minimal memory requirements compared to other tasks (Wolfe, 1998), the observer must at least know what to search for and how to respond appropriately, and must maintain this task set to respond correctly. Similar to some of our theoretical relatives (Bundesen, 1990; Desimone & Duncan, 1995; Duncan, 1996; Bundesen et al., 2005), we propose that working memory plays a vital role in maintaining a target representation and the proper stimulus–response mapping. However, we emphasize the importance of repetition with a specific stimulus–response mapping in a way that models of visual search typically do not. Specifically, we propose that, as an observer repeatedly searches for the same target with the same response set, long-term memory representations drive selection by visual attention and not working memory representations. This hypothesis is derived from extensive research on task automaticity (Logan, 1988).

We recently tested this idea using a behavioral dual-task paradigm with human observers (Woodman et al., 2007). The observers were required to perform a visual working memory task concurrently with a visual search task in which the searched-for target was either the same across trials or changed every trial. We found that when the search target changed from trial to trial there was mutual interference between the search and working memory tasks. However, when the search target identity was the same across trials, minimal interference was observed, replicating previous findings (Woodman et al., 2001b). These findings led us to conclude that visual working memory representations of targets and attended items drive selection by perceptual attention mechanisms in conditions of variable mapping, but in consistent stimulus–response mapping conditions long-term memory representations drive selection. These behavioral findings from humans were also consistent with a study in which the prefrontal cortex of monkeys was lesioned during a similar experimental manipulation (Rossi et al., 2007).

Even a natural behavior such as visually scanning text or an image exhibits signatures of executive control. For example, fixation duration during visual scanning is adjusted strategically according to target–distractor similarity (e.g., Hooge & Erkelens, 1998; Over et al., 2007). These adjustments are based on experience with targets, responses, and consequences.

Encoding, Selection, and Attention

When a complex scene first appears, the signals sweep through the visual system, arriving at a succession of subcortical and hierarchically organized cortical areas (Felleman & Van Essen, 1991; Petroni, Panzeri, Hilgetag, Kotter, et al., 2001; Petroni, Panzeri, Hilgetag, Scannell, et al., 2001). The timing of the arrival of visual signals in different brain structures follows certain patterns. It has long been known that information is propagated through the magnocellular pathway more quickly than through the parvocellular pathway of the visual system (Van Essen et al., 1992). This appears to underlie the observation that areas like the FEF, which is near the top of the hierarchy based on neuroanatomy, can receive visual information very early in time (Schmolesky et al., 1998). Such early information, though, is not very discriminative. Thus, in response to the presentation of a visual search array, neurophysiological studies in parietal and frontal cortex, as well as the superior colliculus, have shown that the first volley of activity following the onset of a visual search array is not selective. By that we mean that the response of a neuron to the stimulus in its receptive field (RF) codes for the low-level visual features of that stimulus and not its task relevance. After this initial indiscriminate volley of activity, a transformation of representation carried by the spiking of the cells occurs, such that neurons with the target or objects similar to the target in their RF are more active and neurons with nontarget objects in their RF become less active (see Figure 9.2).

When the difference in firing rate for neurons with a target versus distractors in their RFs arises, one can say that the target has been selected. Can one say that attention is allocated? Although everybody may know what attention is (James, 1890), the description of attention in the neuroscience literature is rather confused with statements that are mutually incompatible or commit outright category errors. Attention is commonly regarded as a mechanism by which a specific aspect of the environment is selected for scrutiny. It is also said that attention can be directed to different locations or attributes. The basic observation made by many laboratories is that the activity of (certain) neurons in (diverse but not all parts of) the brain is modulated when monkeys (in which the neurons reside) are (said to be) attending. Many authors argue about attention residing in some but not other parts of the visual pathway. But how can attention be both in the visual pathway and directed to an object at a particular location? Also, many authors refer to the effects of attention; thus, for attention to have any effects, it must be causal. In fact, it is not uncommon to read about attention influencing the activity of neurons. However, this cannot be the case, because only neurons (and glia) can influence neurons. Also, if attention causes effects, how can it (at the same time) be directed (as an effect)? For this to make sense, another process must be invoked that moves attention and that causes its effects. But what is this other process? This confusion hinders progress.

It seems sensible to assert that visual-spatial attention ought to refer to the manifestation of a particular brain process or state during the performance of a task in the presence of alternative stimuli or locations. This interpretation seems necessary for the word to have meaningful reference at the behavioral or phenomenal level. Accordingly, the allocation of attention across the visual field need be no more or less than the selective differential activation of neurons in the appropriate network that includes the FEF. In other words, attention can be said to be allocated when certain neurons enter a certain state. Hence, when particular the FEF neurons (as well as neurons in other parts of the network) signal differentially the location of the stimulus of interest, it can be said that attention was allocated. Thus, attention is allocated when and to the extent that the activity of particular neurons represent one as opposed to another location. We will demonstrate below that this operational definition of the allocation of attention can be distinguished in time and neural process from when, whether, and where gaze shifts.

After the initial visual response to the onset of a search array, the stage theory proposes that attention is deployed to locations at which the target is likely to appear in the present context. Of course, if attention is focused on a location in advance of the presentation of the target in a search array, the initial, typically nonselective, neural response can be selective of the location compared to the response to the same stimulus at unattended locations. In addition, preparatory deployments of attention can also be observed in the elevated neural activity of cells representing a specific location prior to the onset of an array (e.g., Woodman et al., in press). In most circumstances outside the laboratory, the focus of covert attention corresponds to the endpoint of a subsequent saccade (Hoffman & Subramaniam, 1995; Kowler et al., 1995). We conceive of free-viewing oculomotor search tasks as equivalent to a sequence of trials beginning with the new fixation location, punctuated by saccades, in which the stimulus remains stable (Motter & Belky, 1998; Findlay & Gilchrist, 2005). That is, the array appears, initial perceptual processing is carried out, attention is deployed to a location, and an eye movement to that location is executed. Of primary importance, we propose that the modulation of visual neurons in sensorimotor structures like the FEF can be identified with the allocation of attention because the neurons modulate in conditions, at the time and to the degree that corresponds to the best psychophysical estimates of where and when attention is allocated in these conditions (Sato & Schall, 2003; Schall, 2004).

Neural correlates of visual selection have been described during a search task in which monkeys were required to make a saccade to a singleton target (e.g., a red stimulus among green distractors, see Schall & Hanes, 1993; Schall et al., 1995; Thompson et al., 1996; Sato et al., 2001). The initial activity of visually responsive neurons did not discriminate whether the target or distractors of a search array fell in the RF, but the later phase of the activity of these neurons reliably differentiated the target from the distractors. This pattern of activity was observed even when the monkeys withheld a saccade (Thompson et al., 1997; Sato & Schall, 2003; Schall, 2004; Thompson et al., 2005). These observations support the hypothesis that the representation of stimuli by visual activity in the FEF corresponds to the allocation of attention (reviewed in Thompson et al., 2001).

Visual search for a target object among distractors often takes longer when more distractors are present. To understand the neural basis of this capacity limitation, we recorded activity from visually responsive neurons in the FEF of macaque monkeys searching for a target among distractors defined by form (randomly oriented T or L) (Cohen et al., 2009a,b). To test the hypothesis that the delay of RT with increasing number of distractors originates in the delay of attentional allocation by the FEF neurons, we manipulated the number of distractors presented with the search target. When monkeys were presented with more distractors, visual target selection was delayed and neuronal activity was reduced in proportion to longer RT. These findings indicate that the time taken by visual FEF neurons to select the target is a likely source of the variation in visual search efficiency.

The findings from recordings of visual neurons in the FEF together with lesion studies indicate that they participate in, and perhaps drive, the selection of targets by a network of areas during visual search. These findings also indicate another possible avenue of inquiry that could link the neural activity in attentional control structures like the FEF to other observations made in cognitive neuroscientific studies of humans performing search. Specifically, electrophysiological recordings from human subjects performing visual search have shown that attention appears to be shifted in a serial manner between the possible target items during the perceptual stage of processing. Woodman and Luck (1999, 2003b) focused on the N2pc component of observers' ERPs to distinguish between parallel and serial models of the deployment of attention during visual search. Some of these models propose that attention is deployed to one object at a time and is rapidly shifted between items during perceptual processing (e.g., Treisman & Gelade, 1980; Wolfe, 2007), whereas other theories propose that perceptual attention is simultaneously deployed to multiple items, and the sequential aspect of processing is how they are entered into short-term or working memory (e.g., Bundesen, 1990; Duncan & Humphreys, 1989; Bundesen et al., 2005). The N2pc is particularly useful for distinguishing between these competing models because it has been shown to index a perceptual mechanism of selective attention that operates prior to awareness and encoding into working memory (Luck & Hillyard, 1994; Woodman & Luck, 2003a). Woodman and Luck (1999, 2003b) showed that, when a visual search task required observers to process items in opposite visual hemifields, the N2pc shifted between hemispheres of the brain. These findings indicate that perceptual attention is shifted between task-relevant items during visual search, consistent with serial models of attentional deployment during search, and ruling out all but the most flexible parallel-deployment models of attention.

It should be possible to test the hypothesis that the visual neuronal activity in the FEF measures the same perceptual selection mechanism indexed by the N2pc in human ERP studies of visual search. That is, future analyses of FEF activity can determine whether or not visual neurons show evidence for serial shifts of selection between possible targets during search; one study has investigated this, but the results are ambiguous because the period of neural activity that was analyzed occurred after the saccade and so cannot contribute to guiding the saccade (Buschman & Miller, 2009). Another approach to understanding the relationship between these neurophysiological metrics of perceptual attention across species of primates (i.e., monkeys and humans) will be discussed below.

A significant thrust of the stage theory is in unifying observations and concepts from psychology and neuroscience. This tenet requires that another type of link be made for a comprehensive understanding of attentional selection during cognitive processing of complex visual information. This empirical link is between electrophysiological studies of attention with humans and with monkeys. The work described here details how electrophysiological studies of activity in the FEF supports the idea that the brain implements cognitive processing using a sequence of distinct stages. Because the FEF entertains bidirectional connections with both dorsal and ventral visual steams of processing and contains neurons that connect to structures that ultimately control the muscles that move the eyes, it is an ideal structure in which to test hypotheses regarding the general nature of information processing in the brain. Electrophysiological studies of humans have been the other main testing ground for hypotheses about the locus of behavioral effects within specific processing stages (e.g., Meyer et al., 1988; Miller & Hackley, 1992; Coles et al., 1995; Vogel et al., 1998; Luck et al., 2000; Woodman & Luck, 2003a). Thus, a central proposal of the stage theory is that findings across these methodological realms must be integrated using a common mode of experimentation.

Building on previous studies that recorded ERPs from nonhuman primates (Arthur & Starr, 1984; Van der Marel et al., 1984; Schroeder et al., 1991; Lamme et al., 1992; Schroeder et al., 1992), several recent studies have sought to directly relate the mechanisms of attentional selection used to study the processing of complex scenes in humans to the mechanisms in the FEF discussed above. Specifically, Woodman, Kang, Rossi, and Schall (2007) recorded ERPs from monkeys performing the difficult visual search task for a T among Ls, or vice versa, mentioned above. Using this task, it was found that monkeys exhibited an ERP component that selected the target item, similar to the N2pc component recorded from humans. Subsequent manipulations and analyses showed that this contralateral measure of selection recorded over extrastriate visual cortex in monkeys exhibited the same sensitivity to cognitive manipulations, had similar relative timing within the sequence of visual ERP components, and had the same distribution across the head as the human N2pc component (for details see Woodman, Kang et al., 2007). We believe the next most useful step involves simultaneously recording activity in the FEF and from the monkey ERP electrodes to directly relate the attention mechanisms measured using these different methods to each other. In doing so, this work will serve to link studies of attention in psychology and neuroscience into a more integrated framework.

Target selection has been measured using a variety of neurophysiological metrics, specifically, using the polarization of local-field potentials (LFPs) in V4 (Bichot et al., 2005) and the FEF (Monosov et al., 2008) and a surface ERP over extrastriate visual cortex in monkeys described above (Woodman, et al., 2007). Is visual selection manifest simultaneously across these different levels of description? Also what temporal relations measured through coherence and other measures are found between spikes and LFP in the FEF and the m-N2pc (e.g., Gregoriou et al., 2009)? Work has begun to address these questions by measuring multiple electrophysiological indices of attention allocation simultaneously. Cohen, Heitz, Schall, and Woodman (2009) recently recorded neuronal spikes, LFPs, and the m-N2pc simultaneously while monkeys performed the difficult T among L (or vice versa) visual search task. They found that the first index of attentional selection that occurred across the neural signals was that carried by the spiking activity of the FEF neurons. Approximately 50 ms later, they observed that the LFPs in the FEF selected the target location. Then, approximately 20 ms after the FEF LFPs, the m-N2pc recorded over lateral occipital-temporal cortex selected the target location. The importance of measuring multiple neural signals of attentional deployment seems self-evident for determining when we can say that attention is allocated to an item during a task. In addition, data such as these are critical to the theoretical question of whether selection is carried out by one or more mechanisms (e.g., Woodman et al., 2001a). However, the methodological details of such experiments are critical given that different neural signals could potentially have different signal-to-noise ratios (Cohen et al., 2009a) or the stimuli used in a task might not be optimal to elicit activity from one or any of the neural measures being collected (Schall et al., 2007).

In summary, we propose that covert attention is shifted between possible target items in the search array until the target for the task at hand is found. This is accomplished by variation in the level of activation of certain populations of visually responsive neurons distributed among multiple cortical and subcortical structures. A central proposition of the stage theory is that this neural state is not necessary or sufficient for the production of an overt response, such as a saccadic eye movement. It is not necessary because saccades can be produced in the absence of any visual stimulation or inattentively. It is not sufficient because attention can be allocated without producing any body movement whatsoever. This independence between stages of processing affords the flexibility of behavior that is particularly apparent in humans and other primates (e.g., Bullock, 2003). We now turn to the neural and cognitive processes responsible for producing movements that can be guided by visual-spatial attention.

RESPONSE PREPARATION

Although the idea of distinct mechanisms performing perceptual-attentional processing and response preparation will not seem controversial to many, this is where the Stage Theory differs drastically from an account of covert attention like the premotor theory of attention.

Although much progress has been made, debate continues over the mechanistic distinction between covert and overt orienting (e.g., Rizzolatti et al., 1987; Klein & Pontefract, 1994; Eimer et al., 2005; Ekstrom et al., 2008). On the one hand, visual attention can be allocated to at least some extent without moving the eyes (e.g., Posner, 1980). On the other hand, several studies have shown that visual attention is allocated to the endpoint of a saccade before initiation of the movement, and that it is difficult to direct attention to a different object even if the object is close to the endpoint of the saccade (Shepherd et al., 1986; Hoffman & Subramaniam, 1995; Kowler et al., 1995; Deubel & Schneider, 1996). Moreover, it has been shown that a shift of attention can influence the production of saccades (Sheliga et al., 1994, 1995; Kustov & Robinson, 1996).

The premotor theory proposes that the deployment of attention is due to subthreshold activity in neurons that control the movements of the eyes. However, we point to four lines of evidence for distinct mechanisms of visual attention allocation and saccade response preparation:

(1) Visual attention and saccade preparation interact but are dissociable (Shepherd et al., 1986; Hoffman & Subramaniam, 1995; Kowler et al., 1995; Sheliga et al., 1995; Deubel & Schneider, 1996; Hooge & Erkelens, 1998; Belopolsky & Theeuwes, in press).

(2) Target selection and the allocation of perceptual attention can occur independently of saccade preparation (Juan et al., 2004, see also Gold & Shadlen, 2003). Visual target selection in the FEF occurs even if no eye movement is produced (Thompson et al., 1997; Schall, 2004; Thompson et al., 2005) or if the saccade is directed away from a conspicuous singleton (Murthy et al., 2009; Murthy et al., 2001; Sato & Schall, 2003; see also McPeek & Keller, 2002). Thompson, Biscoe, and Sato (2005) show an extreme case of this in which monkeys perform a visual search task requiring a manual response. While perceptual processing of the search arrays is occurring, the movement-related neurons in the FEF show activity that is actually suppressed relative to baseline levels.

(3) Neurons that shift gaze can be distinguished from those that select targets (e.g., Murthy et al., 2009). Saccade-related neurons in the FEF produce signals sufficient to specify whether and when a saccade will be produced during the search-step task, but the visual neurons in the FEF that select the location of conspicuous objects do not produce signals sufficient to contribute to the control of saccade generation.

(4) The ability of movement neurons to function independently from the visual selection neurons permits flexible stimulus–response mapping (e.g., Sato & Schall, 2003) and corrective saccades with latencies of less than visual encoding and target-selection time (Murthy et al., 2007). Parallel distinctions are made between ERP components related to early visual processing, attention allocation, and motor preparation (e.g., Coles et al., 1995; Smulders et al., 1995; Woodman & Luck, 2003a).

The dissociation of target selection and saccade preparation was accomplished by training monkeys to produce a prosaccade, an antisaccade, or no saccade, cued by the shape of the color singleton in a visual search array (Sato & Schall, 2003). If the selection process exhibited by visual FEF neurons corresponds to the covert selection of the location of the singleton, then the singleton should be selected regardless of the required response. Moreover, the time of the selection should be the same across the three response conditions. On the other hand, if the process of selection by visually responsive FEF neurons corresponds only to preparation of a saccade, then only the endpoint of the saccade should be selected, and the time of the selection should be affected by the stimulus–response compatibility. Recently, evidence has been produced for both types of neurons in the FEF (Sato & Schall, 2003). Furthermore, when no saccade is produced, many FEF neurons still exhibit selection of the singleton and, later in the trial, many neurons select the endpoint of the unexecuted antisaccade. This modulation for unexecuted saccades cannot be due to bottom-up visual processing and thus must be the product of an endogenous process that can be usefully identified with the allocation of attention coordinated with preparation of the saccade. It is likely that this sequence of attention selection of one object and then another is analogous to the process of attentional shifting that occurs during inefficient visual search tasks (e.g., Woodman & Luck, 1999, 2003b).

This task creates at least a momentary dissociation between the focus of attention and the endpoint of a saccade. In another experiment, saccade preparation was probed by measuring the direction of saccades evoked by intracortical microstimulation of the frontal eye field at different times following the search array (Juan et al., 2004). Saccades evoked in one direction when monkeys are preparing a saccade to a stimulus in another direction exhibit a systematic deviation in the direction of the partially prepared saccade (Sparks & Mays, 1983). This property has been used to probe the preparation of saccades during various tasks (Kustov & Robinson, 1996; Barborica & Ferrera, 2004; Gold & Shadlen, 2003; Opris, Barborica, & Ferrera, 2005). If the premotor theory of attention is correct, then the deviation of saccades evoked at different times in this task should correspond to the level of activation signaling the location of the singleton as compared to the saccade endpoint. Eye movements evoked on prosaccade trials deviated progressively toward the singleton that was the endpoint of the saccade. However, eye movements evoked on antisaccade trials deviated not toward the singleton but only toward the saccade endpoint opposite the singleton. Thus, the visual system can covertly orient attention without preparing a saccade to the locus of attention.

Few would argue that covert orienting of attention and overt orienting of gaze are not guided by common selection mechanisms and coordinated in time (Klein, 1980; Shepherd et al., 1986; Henderson, 1993; Sheliga et al., 1994, 1995; Hoffman & Subramaniam, 1995; Kowler et al., 1995; Deubel & Schneider, 1996; Hunt & Kingstone, 2003; Doré-Mazars et al., 2004; Peterson et al., 2004). The oculomotor readiness or premotor theory of attention has been suggested as an explanation for this relationship. As discussed earlier, one impediment to testing hypotheses generated by this theory has been a lack of precision in specifying the hypotheses. On the one hand, if "mechanisms" and "circuits" refer to particular populations of neurons instantiating a single process, then the results of the Juan et al. (2004) experiment contradict this claim. This conclusion is based on three premises: (1) if an attention shift is just a covert saccade plan and (2) if the monkeys shifted attention to the singleton even in antisaccade trials and (3) if a covert saccade plan is revealed by deviations of evoked saccades, then saccades evoked after the singleton was selected, but before the endpoint was selected, must deviate toward the singleton. We found no such deviation. Therefore, one of the antecedent premises must be incorrect. A literature has been based on the observation that deviations of evoked saccades measure growing saccade plans, and we believe the stimulus properties and task demands offer little room to doubt that the monkeys shifted attention to the singleton. Therefore, by a process of elimination, we can reject the premise that an attention shift is simply a covert saccade plan. On the other hand, if "mechanisms" refer to entire brain structures or circuits comprised of heterogeneous populations of neurons performing different functions (like shifting attention by selecting stimuli and preparing saccades), then our results cannot challenge the theory. However, if the theory is formulated too generally to map onto specific neural populations, then it loses the relevance of mechanism and the force of falsifiability. Thus, these results suggest abandonment or refinement of the premotor theory of attention. We believe that the premotor theory can be regarded as correct insofar as it posits a relationship between saccades and attention that occurs through some overlap between the brain circuits responsible for both. However, it seems clear that a premotor theory based on an identity of saccade planning and attention shifting, such that attention is simply an unexecuted saccade, cannot be correct.

These results and conclusions are important for understanding an important recent observation concerning the role of the FEF in attention allocation. Weak electrical stimulation of the FEF in macaques improves the allocation of attention at the location corresponding to the endpoint of the saccade that would be evoked with stronger stimulation, and this occurs through an influence on the activity of neurons in extrastriate visual area V4 (Moore & Armstrong, 2003; Moore & Fallah, 2004; Armstrong et al., 2006). This result has been interpreted as strong evidence in support of the premotor theory of attention, but the evaluation of this claim must be framed by the anatomical connectivity between the FEF and V4. Specifically, is the influence on V4 exerted by the population of neurons in the FEF that also delivers saccade command signals to subcortical structures? We recently addressed this question anatomically by analyzing the pattern of neurons labeled by retrograde tracers placed in V4 and the superior colliculus (SC; Pouget et al., 2009). The strongest evidence for the premotor theory of attention would be finding individual neurons in the FEF projecting to both the SC and V4. However, we found no neurons in the FEF projecting both to SC and V4. In the FEF, all neurons innervating SC are located in layer 5, whereas the large majority of neurons innervating extrastriate visual cortex are located in supragranular layers (see also Barone et al., 2000). The conjunction of physiological and anatomical findings suggests that the signal conveyed from the FEF to extrastriate visual cortex does not correspond to saccade preparation but instead can be identified with the allocation of visual spatial attention. The functional insights afforded by these anatomical results illustrate the utility of the stage theory of attention and action in organizing diverse kinds of data.

Further evidence for the stage theory was obtained by examining the timing and pattern of visual target selection and saccade preparation in a task that required observers to respond to random changes of target location on some trials. The search-step task combines a standard visual search task with the classic double-step saccade task. On most trials (referred to as no-step trials) observers were rewarded for making a saccade to a color oddball target among distractors. On the remaining trials (step-trials), the target and one distractor unexpectedly swapped positions after presentation of the array. When the target stepped from its original position to a new position, observers were rewarded for directing gaze to the new target location (compensated trials). However, observers often fail to compensate for the target step and made a saccade to the original target location (noncompensated trials). In other words, they shift gaze to a location different from that occupied by the target. This behavior is not rewarded. We have shown that performance of macaque monkeys and humans is qualitatively indistinguishable and can be understood as the outcome of a race between a process that produces the first saccade, a process that interrupts the first one, and a process that produces the second saccade (Becker & Jürgens, 1979; Camalier et al., 2007).

Noncompensated saccade trials provided data to test the dissociation of visual target selection from saccade preparation. Even when gaze shifted away from the popout oddball of the search array, visual neurons in the FEF represented the current location of the target (Murthy et al., 2009). Further evidence for a functional dissociation of visual selection and response preparation was obtained in the trials in which the target stepped out of the receptive or movement field, and monkeys canceled the initial saccade to redirect gaze to the final target location. Whereas the visual neurons continued to discharge as if no stimulus change had occurred, the movement neurons were strongly modulated early enough to control the initiation of the saccade (Murthy et al., 2009).

The search-step task provides still further evidence that saccade preparation and production can be accomplished without or in spite of visual processing. During target-step trials, after generating the error saccade to the original target location, humans and monkeys commonly produce corrective saccades to the final target location. Many of these corrective saccades are initiated with latencies that are so short (<100 ms) relative to the error saccade that they could not be guided by the outcome of visual processing. Nevertheless, the latency of these corrective saccades is predicted by the timing of movement-related activity in the FEF. Preceding rapid corrective saccades, the movement-related activity of neurons began before visual feedback of the error could be registered. Moreover, the movement-related activity of a few neurons began even before the error saccade was completed (Murthy et al., 2007).

Although perceptual and response processes can be dissociated, the ultimate RT of saccades is partially determined by the duration of processing at the perceptual stage. The contribution of target selection time during perceptual processing to the variability of saccadic response latency varies with target discriminability and task demands (Thompson et al., 1996; Bichot et al., 2001; Sato et al., 2001; McPeek & Keller, 2002; Sato & Schall, 2003; Ipata et al., 2006; Shen & Paré, 2007; Thomas & Paré, 2007; Balan et al., 2008; Cohen, Heitz et al., 2009). For example, during feature-search tasks for a red target among green distractors (or vice versa), the time that elapses between the initial volley of visual activity and when the visual cells in the FEF select the feature target accounts for a small proportion of the ultimate trial-to-trial variability in reaction time (RT; Sato et al., 2001). However, when macaques search for a complex form-defined visual target (e.g., a rotated T among randomly rotated Ls), a much larger proportion of the RT variability is accounted for by the variance in the measure of perceptual processing by visual cells in the FEF (Cohen, Heitz et al., 2009). Next, we turn to the issue of how information is transmitted from the network of neurons that carry out perceptual processing to those that perform response-level processing.

The issue of interstage information transmission has received a significant amount of study by cognitive psychologists using electrophysiological methods but often is absent from the neuroscience literature. One critical and contentious issue regarding the flow of information through different stages of information processing is whether processing at one stage is completed before information is transmitted to the next stage. The competing cognitive architectures that have been proposed are often referred to as *discrete versus continuous models* of information processing (Miller, 1982; Meyer et al., 1984; Meyer et al., 1988). Guided by Donders' ideas, Sternberg (1969b) proposed that information was transmitted in a discrete manner between the stage of perceptual processing and subsequent stages, such as the stage of response selection. This framework was extremely effective in accounting for RT effects in different paradigms and has provided an effective way to interpret results from a variety of cognitive tasks (Sternberg, 1984). However, subsequent cognitive models have shown that the same findings from RT experiments can be accounted for with overlapping stages of processing (McClelland, 1979). Because both types of models can account for behavioral data with similar success it is not possible to distinguish between these categories of models with RT data alone.

In fact, it was recognized that partitioning RT into constituent stages could not be done conclusively without some way of measuring the termination or initiation of covert stages. Research over the last 30 years or so—and especially in the last 10 years—has demonstrated how to solve this measurement problem. The approach uses physiological measures that are believed to correspond to or index the timing of particular cognitive processes. This was addressed first with ERPs, but single-unit recordings from monkeys performing tasks like visual search have provided equally useful information. Typically, studies focused on distinguishing between discrete or continuous flow models have measured the timing of the P3 component, to index the end of perceptual processing (also called *stimulus evaluation time*; for a review see Coles et al., 1995) or the LRP, which indexes response preparation (Coles et al., 1988; Miller & Hackley, 1992; Osman et al., 1992; Miller & Schroter, 2002; Rinkenauer et al., 2004). The results of these experiments have indicated that it is possible for information to flow continuously between stages of perceptual and response processing. However, as Miller and colleagues have pointed out, the evidence is also consistent with a model in which information about individual features of a stimulus can be processed independently with different time courses, and when one feature is processed it is transmitted to the response stage (Miller, 1988; Miller &

Hackley, 1992). We have found this model of interstage information transmission to be effective in accounting for findings from unit recordings from the FEF during visual search and other tasks.

A series of studies have sought to understand the nature of interstage information transmission by recording from neurons in the FEF of monkeys performing attention-demanding tasks (Sato et al., 2001; Woodman et al., 2008). The findings from these studies are consistent with the view that response processing does not begin until perceptual processing is completed (e.g., Woodman et al., 2008), but these conclusions are tentative (see Bichot et al., 2001) and appear to be sensitive to the number of features defining the target. The studies performed thus far used neuronal recording techniques in which activity from a single neuron or a small number of similar neurons was recorded at the same time (see also Mouret & Hasbroucq, 2000). This means that neurons instantiating covert target selection and those instantiating saccade response processes were recorded at different times. Firm conclusions about the flow of information between computational stages will require future studies to record the neural activity indexing processing in different stages simultaneously. The stage theory points to this empirical gap in our knowledge as critical for describing how cognitive subsystems work together.

After information is transmitted to the network of neurons that controls the physical movement of the eyes, the appropriate saccade must be prepared and initiated. When saccade preparation is carried out, movement cells in the FEF exhibit a build-up of activity preceding the saccade that results in an eye movement fixating the target location (Hanes & Schall, 1996). During free-viewing search, the process of saccade preparation would occur after each item receives the benefit of a covert shift of attention (Hoffman & Subramaniam, 1995; Kowler et al., 1995).

In a recent study, we showed how measuring different aspects of the activity in these saccadic response cells in the FEF could be used to quantify different constructs described in many cognitive models of attention, categorization, and decision. Woodman et al. (2008) analyzed the spiking activity recorded from movement-related neurons in the FEF during a variety of visual search tasks (color and motion feature-search tasks and search for form-defined targets) and related these different neural metrics to the RT effects that were observed. We measured four different characteristics of the neural activity. First, we measured the baseline-firing rate of these cells prior to the presentation of the visual search array. This metric provides an estimate of the degree to which neurons coding for a specific response (i.e., a saccade into the movement field of the neuron) are biased prior to the beginning of the trial. Because responses in any direction were equally likely, we expected not to find any systematic biases in response direction prior to the response. Next, we measured the time of the onset of the build-up of activity preceding the saccadic response. This served as a measure of the beginning of the response stage of processing that prepares the ultimate behavioral response to the search array. Third, we measured the slope of the build-up of activity in these saccadic response-related neurons. This served as a concrete measure of the rate at which information accrued at the response stage. Finally, we measured the activity level in the interval immediately preceding the saccadic response (i.e., the 20 ms before the saccade into the movement field). This provides a measure of the threshold for neural activity in these movement-related cells, the crossing of which causes the saccade to be triggered (Hanes & Schall, 1996). We found that saccadic-response variability during visual search was best accounted for by delays in the onset of the response stage. This finding is consistent with models of visual attention that propose that search tasks heavily tax perceptual attention mechanisms but not response or memory subsystems (Wolfe, 1998). This study provides an example of linking components of cognitive models to specific neural markers in order to provide definitive tests of models of processing.

Performance Monitoring

At the moment when the saccadic response is made, the trial is over, but cognitive processing is not. The response was either correct, in that the target was fixated, or an error was made. In experiments with monkeys, this means that reward is delivered when the behavior was correct and withheld when the response was wrong, which provides explicit feedback regarding task performance. However, in many experiments with human observers, no feedback about task performance is explicitly provided. Does the brain know if the task was performed correctly? If so, how does this information about the outcome of performance change how information is processed on the next trial?

There is now abundant evidence that the brain has an extensive performance-monitoring network. In humans, electrophysiological studies have shown that, if an observer makes an error, the brain registers this incorrect performance immediately after the response. Response-locked ERPs indicate that when an error is made, a medial-frontal negativity is recorded and often followed by a positivity with a more parietal distribution (Gehring et al., 1993; Falkenstein et al., 2000; Gehring & Willoughby, 2002). The error-related negativity (or ERN) has been interpreted to index error detection (Gehring et al., 1993), response conflict (Botvinick et al., 2001), or dopamine-regulated learning signals (Holroyd & Coles, 2002; Brown & Braver, 2005). It has been proposed that this error signal may arise from the anterior cingulate cortex (ACC) and is used to modify how information is processed on the subsequent trial. However, it remains an open question whether such adjustments in how information is processed are focused on perceptual processing, the response stage, or both. In other words, which stage(s) does the executive control? And how?

Unit recording studies suggest that neurons in the performance-monitoring network may preside over more areas than just ACC. Specifically, neural activity recorded in the supplementary eye field (SEF) consistently shows evidence for error- and reward-related modulations following the response in a task (Stuphorn et al., 2000). The causal influence of the SEF on performance of oculomotor control tasks has been demonstrated using microstimulation in macaque monkeys. Stuphorn and Schall (2006) examined the behavioral performance of monkeys during the ocular–motor countermanding paradigm immediately following the delivery of microstimulation of the SEF. They found that this stimulation caused the monkeys to behave more conservatively compared to baseline performance trials without microstimulation. In particular, the monkeys' saccadic RT was increased, so that error rates were reduced following weak microstimulation of the SEF. This shows that the SEF is part of the network that monitors performance and controls the visual and motor subsystems that perform perceptual and response processing. At this point, it is unclear whether the performance monitoring and control network only includes medial and dorsal cortical structures (such as ACC and SEF), or whether the network of areas implementing these functions is more widespread. For example, intracranial recordings of electrical potentials in human patients (Halgren et al., 2002; Wang et al., 2005) have suggested that regions of the parietal lobe also produce error-related activity and may be a part of a broad network that evaluates the outcome of behavioral responses and influences future processing. Similarly, imaging studies of normal human observers have implicated regions of the inferior frontal cortex in performance monitoring and control functions (Aron et al., 2004). Clearly, the research examining the localization versus distribution of cognitive monitoring and control functions is ongoing.

In summary, even after the trial is over, cognitive processing continues. This could be thought of as the most recently discovered stage of processing, as it has become the focus of cognitive models only in the last decade (e.g., Botvinick et al., 2001; Holroyd & Coles, 2002; Brown & Braver, 2005). Based on the density of connections of medial frontal areas with motor areas (such as the FEF) and the paucity of connections with extrastriate visual areas, we hypothesize that the product of this stage is attenuation or facilitation of the response preparation process. By changing the willingness to respond, by speeding or slowing the response preparation process, the executive control network can enable speed at the cost of accuracy or vice versa.

RELATIONSHIP TO OTHER THEORIES

In its attempt to be comprehensive, the stage theory of attention and action relates to and expands on other major theoretical approaches in cognitive psychology. Certainly, the proposition that selective processing can occur according to stimulus and task demands within any of a sequence of processing stages is similar to proposals that have shaped debates for some time and remain vibrant avenues of research (Luce 1986; Meyer et al., 1988; Luck & Hillyard, 2000; Sternberg, 1969a, 2001). Some models gain specificity at the cost of scope. For example, stochastic models of RT in target discrimination tasks explain the systematic variability of RT and choice entirely in terms of sequential sampling of perceptual evidence. Errors produced by the response stage are not accounted for in these models. However, the FEF visual neurons select the target correctly even when monkeys make errors with the eyes (Murthy et al., 2001; Murthy et al., 2009) or hands (Trageser et al., 2008). Meanwhile, stochastic models of RT and choice in stimulus perturbation tasks (like stop signal or double-step) explain the systematic variability of RT and choice effectively in terms of a race between alternative response channels (Logan & Cowan, 1984; Camalier et al., 2007). Independent race models can be implemented in neural networks with the proper temporal pattern of interaction (Boucher et al., 2007; Lo et al., 2009). However, the input to these models is unspecified.

Current stochastic accumulator models implement speed-accuracy adjustments through strategic changes of the threshold of the accumulation process (Smith & Ratcliff, 2004; Gold & Shadlen, 2007). The evidence for distinct stages of processing suggests that speed–accuracy adjustments can be accomplished through changes of the visual selection stage or the saccade preparation stage, or both. The neural mechanism(s) of speed–accuracy adjustments is not understood. Signal detection theory (Green & Swets, 1966) and biased choice theory (Luce, 1986) both distinguish sensitivity, which is limited by the sensory apparatus, from response bias, which is the willingness to respond. The statement "willingness to respond" seems to point very clearly to the mechanism of speed–accuracy adjustment.

How can sequential sampling models of perceptual evidence (target vs. distractor) and race models of response production (saccade here vs. there) be integrated? Are they different descriptions of one process? Or, are they descriptions of different processes that operate in succession? In general, numerous models of visual search have been developed, but the models have fundamentally different architectures (e.g., Bundesen, 1998; Hamker, 2004; Wolfe, 2007). It is difficult or impossible to decide between alternative models based only on behavioral data (e.g., Van Zandt et al., 2000). We advocate the proposition that appropriate neurophysiological data can discriminate between alternative mechanisms if proper linking propositions are established (Schall, 2004; Teller, 1984).

CONCLUSION

The stage theory of attention and action is proposed with the aim of organizing and integrating a diverse and often bewildering collection of observations, hypotheses, and suppositions. Beyond the possible unification of disparate views, it is hoped that the stage theory identifies important questions to answer with investigative techniques that provide greater anatomical, conceptual, and temporal resolution. We are optimistic that such research will reveal the cognitive and associated neural processes responsible for selecting targets on which to allocate attention and to which to shift gaze.

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