Neural correlates of visual and motor decision processes

Jeffrey D Schall* and Narcisse P Bichot

Recent research has clarified and revealed characteristics of perceptual and motor decision processes in the brain. A democracy of sensory neurons discriminate the properties of a stimulus, while competition contrasts the attributes of stimuli across the visual field to locate conspicuous stimuli. Salience and significance are weighed to select an object on which to focus attention and action. Experimentally combining neural and mental chronometry has determined the contribution of perceptual and motor processes to the duration and variability of behavioral reaction time. Whereas perceptual processing occupies a relatively constant amount of time for a given stimulus condition, the processes of mapping particular stimuli onto the appropriate behavior and preparing the motor response provide flexibility but introduce delay and variability in reaction time.

Addresses
Vanderbilt Vision Research Center, Department of Psychology, Wilson Hall, Vanderbilt University, Nashville, Tennessee 37240, USA
*e-mail: jeffrey.d.schall@vanderbilt.edu

Abbreviations
ERP	event-related potential
FEF	frontal eye field
MT	middle temporal visual area
V1	primary visual cortex

Introduction

"To succumb to the preponderance of one set of influences over another set", as Ambrose Bierce [1] characterized decision, may be an accurate summary of recent evidence from behavioral neurophysiology experiments. Although complex decisions are difficult to investigate, the decision of where to direct gaze and grasp has proven particularly accessible experimentally. Visual selection and attention have been reviewed recently [2–5], so we will emphasize work, framed by recent studies in our laboratory, on neural processes associated with saccade target selection and gaze control in the frontal eye field (FEF).

Vision with scanning eye movements

The decisions made by the visuomotor system of primates must be considered in light of the natural behaviors produced in ecological settings. To identify an object in a scene, the eyes move so that the image of the object falls on the fovea. Saccadic eye movements are the rapid shifts of gaze that redirect the visual axis onto a new point in the image. Saccades tend to direct gaze to conspicuous features in the scene, but knowledge and goals also strongly influence the focus of gaze [6]. Although the relationship between cognitive states and the patterns of scanning eye movements has proven difficult to elucidate [7], recent studies have shown systematic relationships between gaze behavior and information acquisition for visually guided behavior [8].

Visual search tasks, employed for many years to investigate visual attention, have been used recently to investigate saccade target selection [9,10]. The results of these studies have provided strong evidence for distinguishing the process responsible for selecting the target where gaze will shift from the process regulating when gaze will shift [11••]. Other recent studies have demonstrated clearly that the focus of attention coincides with the target of an intended saccade [12,13•] and that directing attention can influence the production of saccades [14••,15]. These results indicate that a common visual selection mechanism governs both covert and overt orienting. This conclusion is supported by recent brain imaging studies showing that common regions in human frontal and parietal cortex are activated in association with attention and saccade tasks [16,17]. At the same time, it is important to remember that the relation between attention and eye movements is not obligatory. In fact, covert orienting may be little more than a state of visual selection without activating motor circuitry to produce overt orienting.

Normal visual behavior is accomplished through a continuous cycle of fixation and visual analysis interrupted by saccades. During fixation of one point in the image at least three processes take place. One process is the visual analysis of the image centered on the fovea to ascertain its identity. The other two are the visual analysis of the image in the periphery to locate potential targets for the next saccade, and the production of the saccade. Several key questions provide a framework for investigating the dynamics of visually guided behavior [18]. Namely, how much time does perceptual processing and response preparation take? Can these two processes overlap? How late can perceptual processing influence response preparation?

Neural correlates of saccade target selection in the FEF

Evolution of target selection signals

To investigate how the brain selects the target for a visually guided saccade, neural activity has been recorded in the FEF of monkeys making saccades to the oddball target in a popout visual search task [19,20••,21••,22•] or scanning complex images [23]. The FEF is an interesting area in which to investigate sensory decision processes because it is reciprocally connected with many extrastriate visual areas associated with both the dorsal and ventral visual streams [24], and also because it projects directly to

brainstem oculomotor structures [25,26]. Thus, the FEF is a nodal area, positioned to sample and possibly influence the outcome of visual processing and to play a central role in the production of eye movements [27,28•].

We found that the initial response of most visual neurons in the FEF did not discriminate whether the target or only distractors of the search array appeared in their receptive field (Figure 1a) [19,21••]. This observation should not be surprising because earlier work had shown that the visual responses of FEF neurons are typically not selective for the properties of stimuli [29]. However, before saccades were generated, a discrimination process occurred by which the activity of visually responsive cells in the FEF evolved to signal the location of the oddball target regardless of the visual feature (e.g. color or form) that distinguished it from the distractors.

During our studies on saccade target selection in the FEF of macaques, we found that the target selection signal that arises in the FEF had a number of interesting properties [19]. First, the initial response to an array of stimuli was consistently attenuated relative to the initial response to a single stimulus. This attenuation may have been attributable either to suppressive interactions among stimuli or to uncertainty about the location of the target. A similar finding has recently been made in the superior colliculus [30]. Second, target selection was achieved by a reduction of the activity evoked by the distractors (even though they were still in the receptive field), leaving only cells with the target in their receptive field with maximal activity. The current data do not indicate whether selection is accomplished through passive decay of distractor responses coupled with enhancement of the target response or through active suppression of the distractor responses [31•]. Third, the magnitude of the suppression of distractor-evoked activity varied with the proximity of the target to the receptive field, often being greater if the target flanked the receptive field. Behavioral studies have indicated that distractors close to a target are less likely to be selected than are more distant distractors under some [32], but not all [9], conditions; a center-surround selection mechanism has also been inferred in more complex cognitive decisions [33].

Effects of experience on target selection processes
Experts are more likely than novices to ignore conspicuous but non-informative elements of a visual image from their area of expertise [34]. This observation emphasizes the extent to which attention and gaze are under voluntary control. The degree of control and the rules by which it is expressed are being clarified by recent behavioral studies. Some studies indicate that salient stimuli in search displays attract attention automatically [35,36]; however, other work indicates that cognitive strategies can prevent the capture of attention by salient stimuli [3,37]. Other behavioral studies have demonstrated that search is

facilitated by implicit or explicit knowledge of the target properties [38] or location [39••].

We recently found that the neural selection process expressed in FEF can be modified profoundly by differences in cognitive strategy derived from experience [20••]. The findings from FEF described above were made in monkeys trained to search for an oddball stimulus regardless of the particular visual feature that defined it (e.g. both a red target among green distractors and a green target among red distractors). To perform the task, the monkeys had generalized a strategy of searching for the oddball stimulus. We found that when monkeys were given exclusive experience with one visual search array (e.g. only red among green), they adopted a strategy of ignoring stimuli that were distractors, even when those same stimuli became the oddball target in the complementary visual search array (e.g. green among red). In monkeys employing this behavioral strategy, we discovered that half of the visually responsive cells in FEF exhibited a suppressed response to the learned distractor as soon as the neurons responded. In other words, these neurons, which in earlier work had responded indiscriminantly to the target or distractors, now exhibited an apparent feature selectivity in their initial responses completely unlike what had been observed before in FEF. This finding may be related to earlier demonstrations of visual discrimination in prefrontal cortex based on instructions [40–42]. In summary, the physiological and anatomical data indicate that FEF may be regarded as a saliency map, a representation of the visual field in which the location of potential targets are registered, tagged by both feature properties and prior knowledge or expectations. What is the visual input to such a saliency map?

Visual analysis and selection
A visual image must be analyzed to provide information necessary to guide gaze. It is useful to distinguish different kinds of visual analyses. Beyond simply detecting the presence of visual stimuli, a higher level of analysis discriminates between alternative interpretations of a visual element at one retinal location. A still higher level of analysis compares visual elements across the visual field to select conspicuous or behaviorally relevant elements. Neural correlates of stimulus discrimination and stimulus selection have been investigated and are described below.

Stimulus discrimination
The relationship between visual neural responses and behavioral discrimination has been investigated extensively [43–45,46••]. Modeling efforts based on data from the middle temporal visual area (MT) indicate that perceptual decisions can be based on the weakly correlated activity of small populations of neurons, not all responding optimally, combined through a somewhat noisy process to signal one of the alternative directions of motion [47•]. A critical question is how do other centers in the brain 'read out' the activity of sensory cortex. It appears that the decision

Figure 1
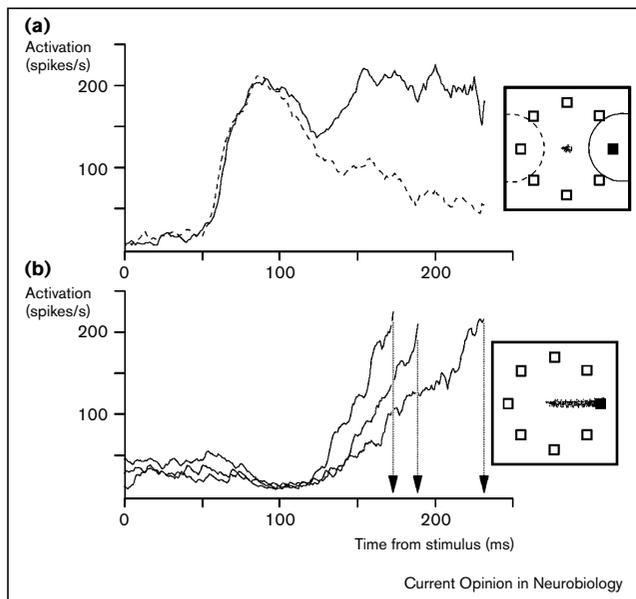
Target selection and saccade production by FEF. **(a)** Comparison of activation of a visually responsive FEF neuron during visual search when the target of the search array was in the receptive field (solid line) and when only distractors of the search array were in the receptive field (dashed line). The locus of fixation is shown on a representative visual search display. Although the plots of activity were derived from one neuron, the visual search display shows receptive fields at two locations, one enclosing the target (solid semicircle) and the other enclosing a distractor (dashed semicircle), to illustrate the visual input to the neuron on the different types of trials. The initial visual response does not distinguish whether the target or distractors of the search array appeared in the receptive field. Over the next 100 ms, the activity evolves to signal whether or not the target was in the receptive field. Adapted from [21••]. **(b)** Stochastic growth of movement-related activity in FEF before saccades. Movement-related activity of a FEF neuron is plotted from trials that had three ranges of saccade latency. The plots of activity stop at the instant of saccade initiation, which is indicated by the arrows. Saccadic eye movements to the target are shown on the search display. Adapted from [73••].

rule depends on the context of the behavior. When a graded response is called for, then vector averaging appears to be used, but when categorical responses are required, a winner-take-all mechanism is employed [48,49••,50]. The balance of speed versus accuracy influences the decision rule: responses following short reaction times tend to reflect the outcome of an averaging decision, whereas responses following longer reaction times reflect a winner-take-all rule. This relationship is commonly observed for saccades made when multiple stimuli are presented [9].

Usually, a given stimulus arrangement supports a unique perceptual state. However, certain stimulus configurations that are perfectly discriminable support mutually exclusive perceptual states, such as the Necker cube or binocular rivalry. It has proven possible to relate the responses of neurons to ambiguous stimuli to the alternative perceptual

states reported by monkeys [51]. The correlation between neural activity and perceptual report improves as signals are conveyed further from the retina [52,53••]. These results indicate that when confronted with equally viable but competing interpretations of the image, the visual system does not tolerate ambiguity but adopts one of the alternative interpretations.

Stimulus selection

Visual elements can be selected on the basis of properties distinguishing them from surrounding elements or on the basis of prior instructions. Neural correlates of both kinds of visual selection have been described. Recent studies have demonstrated that a population of neurons in striate cortex is sensitive to local stimulus irregularities [54] and global texture gradients [55••]. In addition, a number of recent studies have investigated how the responses of cells in primary visual cortex (V1), extrastriate areas V2 and V4 [56••,57•], MT and MST [58], posterior parietal cortex (LIP and area 7a) [59•,60–62] and rostral inferior temporal cortex [63] are modulated according to the task instructions of what stimulus property or visual field location to attend to guide the behavioral response. Generally, responses to attended stimuli are greater than responses to unattended stimuli, accounting for intrinsic stimulus preferences. This modulatory effect appears to be more pronounced in areas further removed from V1 and is commonly greater if multiple stimuli are in a neuron's receptive field.

The mechanisms of the various forms of extraretinal modulation are not known. One informative avenue for elucidating the contributions of different mechanisms is examination of the time course of the modulatory effects both within the response of a single trial and across multiple trials as goals change. Unfortunately, many studies do not provide detailed information about the time course of the modulation for individual cells, although there are exceptions. For example, the long latency and spatial extent of the global texture effect observed in V1 [55••] suggests that it originates in feedback from extrastriate visual areas. Also, when stimuli were presented sequentially, the effects of attentional allocation were evident as soon as V4 neurons responded, but when multiple stimuli were flashed simultaneously, then attentional modulation was delayed slightly [56••]. Under both conditions, however, the attentional modulation of V4 neurons was multiphasic, with more pronounced modulation appearing 100–200 ms after stimulus presentation; such patterns are suggestive of different sources of modulation. Now, as we learn more about the time course of visual selection in different areas of the brain, it will be important to relate the different phases of selection to behavioral reaction times.

Time course of saccade target selection

The duration and variability of experimental reaction times or natural fixation periods exceed what can be

accounted for by simply adding transduction and transmission times from the sensory surface to the muscles [64]. Experimental psychology began with the hypothesis that reaction times are composed of stages of processing, and many behavioral studies have been conducted to investigate the flow of signals between these stages [65–67]. However, the conclusions of these behavioral studies are limited because they lack clear markers for the end of one stage and the beginning of another. Physiological measures can provide such markers. For instance, using event-related potentials (ERPs), investigators have deduced that the P300 component represents the conclusion of perceptual processing, and the lateralized readiness potential represents response preparation [68]. Unfortunately, the lack of spatial resolution and of knowledge of the neural generators of ERPs limit conclusions that can be drawn from these studies. To investigate stages of processing with the highest spatial and temporal resolution, single-neuron recording work can be guided by the insights of ERP studies inspired by psychological theories.

Having found that saccade target selection by FEF neurons occurred over time, we reasoned that a good marker for the conclusion of perceptual processing was the time at which FEF neurons registered whether the target or only distractors were in the response field [21••]. We related this time to variations in saccade latency and found that most visually responsive FEF neurons discriminated the target from distractors at a fairly constant interval after stimulus presentation (Figure 2). In other words, the time at which FEF neurons discriminated the target of the search array did not predict when gaze would shift to the target. In fact, FEF neurons discriminated the salient oddball stimulus from distractors even if monkeys never shifted gaze to the oddball target of a search array [22•]. Therefore, if the time of target discrimination by FEF neurons indexes the outcome and conclusion of perceptual processing, then it appears that although perceptual processing occupies a good portion of the reaction time, an additional delay and much of the variability of reaction time is unaccounted for. Thus, a postperceptual stage of response preparation must introduce the additional delay and variability observed in reaction times. This finding is consistent with conclusions from ERP studies [68] and substantiates the decoupling between perceptual processing and response preparation that has been observed in behavioral studies [11••,12]. This finding also suggests the possibility that the period after the target has been discriminated but before the saccade is produced may be the state in which attention has shifted to the location of the target.

From perception to action

Discrimination of sensory stimuli, while admittedly complicated and not fully understood, is still just the first step. If it is to guide action, one of the discriminated objects must be selected. But once an object is selected in the

Figure 2
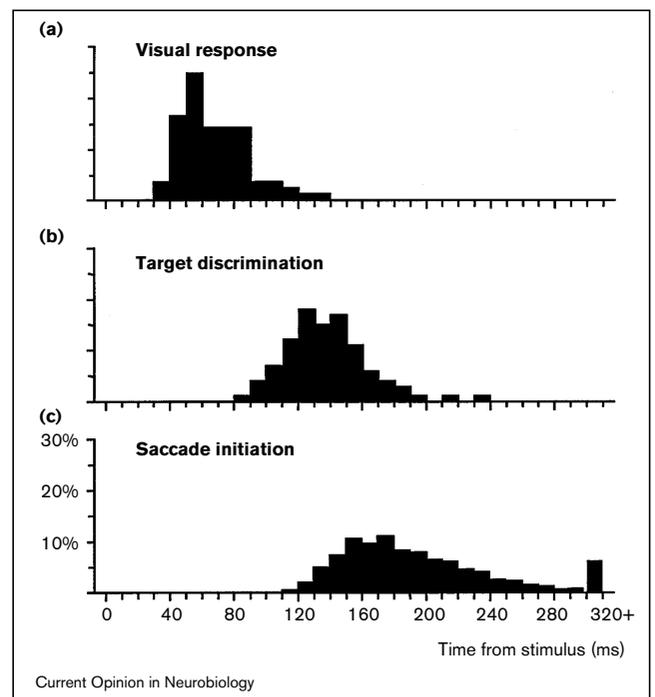
Neural and behavioral chronometry. **(a)** Visual response latencies indicate when neurons in FEF became activated following presentation of the visual search array. The initial response did not discriminate the target from distractors. **(b)** The time of target discrimination indicates when the activity of FEF neurons reaches a state that is a statistically reliable signal of whether the target was in the response field. **(c)** Saccade initiation time measures when monkeys shifted gaze to fixate the selected target. During simple visual search, the time at which most FEF neurons discriminated the target did not predict when the eyes would move.

image, what is to be done with it? Approach or avoid? Look or not look? Grasp or not grasp? Because a given stimulus can afford different actions depending on experience and goals, it is necessary to distinguish the process that asks 'What is there?' from the process that asks 'What to do?'. The stage of processing in which the second question is answered is response selection and preparation. Several neurophysiological studies have investigated how particular stimuli become mapped onto arbitrary behaviors [69–71,72••]. The results of these studies uniformly demonstrate an evolution of neural activity during the reaction time from an early representation of the location of the sensory cue stimulus to a later representation of the direction of movement. Each study also identified neurons representing more complex contingencies of sensory and tonic activity on the stimulus–response mapping rule.

Once a behavioral response has been selected, the remaining decision to make is when to move. For gaze shifts, this is accomplished through the delicate balance of gaze-holding and gaze-shifting mechanisms in the oculomotor system. We have recently analyzed movement-related activity recorded in the FEF to evalu-

ate alternative models of reaction time [73••]. As illustrated in Figure 1b, we found that saccades were initiated when movement-related activity in the FEF reached a particular level that did not vary with saccade latency. Similar conclusions have been drawn from lateralized readiness potentials [74], from recordings in premotor and primary motor cortex [75], and in superior colliculus [76,77]. Thus, if the trigger mechanism for movement has a fixed threshold, then what can account for the stochastic variability of reaction time? In single-unit data from FEF [73••], the variability in reaction time appears to be accounted for by variation in the rate of growth of the premovement activity, which began at a fairly constant interval after target presentation, towards the threshold. In other words, trials with longer reaction times occurred when the rate of growth of the premovement activity was slower than on trials with shorter reaction times. The movement-related neural activity in FEF closely resembles the elements of models of reaction time [78,79].

Conclusions

Decisions transpire over time as multipotentiality gives way to determination. This review has described recent studies that have identified neural correlates of this transition in perceptual and postperceptual stages of processing. By emphasizing the chronometric approach, neuroscience and cognitive psychology can collaborate fruitfully to provide a fuller understanding of how the brain makes decisions. In all likelihood, the mechanisms revealed by studies of perceptual decisions may well apply to more portentous decisions.

Acknowledgements

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Monkeys responded to slowly moving light spots by generating pursuit or saccadic eye movements. The accuracy of the eye movements depended on the estimation of the stimulus velocity. Normal performance was compared with performance when loci with known motion direction preferences in area MT were electrically microstimulated. The pattern of eye movement responses in most cases indicated that the velocity signal generated by the microstimulation was combined in a vectorial fashion with velocity signal derived from the visual stimulus. This evidence for a vector-average decision rule contrasts with a winner-take-all decision rule revealed by another study using microstimulation of area MT in monkeys performing an eight-alternative forced choice direction of motion judgement [50]. Evidently, the decision rule employed adapts to the opportunities and demands of the current situation.

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