THE NEURAL BASIS OF SACCADE TARGET SELECTION

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Abstract

The neural basis of saccade target selection reviews how the visual system locates objects that are salient through their visual features relative to surrounding objects or through their importance based on task goals and then produces an appropriate overt response like a gaze shift. The neural processes responsible for locating salient or important locations and producing saccades occur in a large number of visual and visuomotor structures and cortical areas. We will describe findings from primary visual cortex and extrastriate visual areas that represent object features and findings from the parietal lobe, the superior colliculus and the frontal eye field that represent target salience and generate motor commands.

Keywords

1 attention
2 salience map
3 frontal eye field
4 stages of processing
5 neural chronometry

“It would be an important subject of pedagogical methodology to provide firm and necessary rules for the perceptual activity of the eye” (Purkinje 1819, in Wade and Brožek 2001).

Introduction

Primate visual behavior is organized around a fovea which provides high acuity vision over a limited range of the central visual field. Consequently, to identify an object in a scene, gaze must shift so that the image of that object projects onto the fovea. Because gaze can be directed to only one place at a time, some process must distinguish among possible locations to select the target for a saccade. Consequently, some items may be overlooked. The outcome of the selection process is purposeful in the context of visually guided behavior (see Chapter 29 by Hayhoe). As reviewed elsewhere in this volume, patterns of eye movements express regularities such as concentrating on conspicuous and informative features of an image under diverse conditions (see Chapters 26, 27, 28 by Reingold, Ekstein and Geisler).

This chapter will review our current understanding of the neural basis of saccade target selection. The process of selecting the target for pursuit eye movements is similar (see Chapter 8 by Barnes). This topic has been reviewed by ourselves and others recently (Schall et al. 2003; Schall 2003, 2004a; Schiller and Tehovnik 2005; Thompson and Bichot 2005; Bichot and Desimone 2006; Fecteau and Munoz 2006), so this chapter will frame the major issues and highlight more recent developments.

Visual Search, Selection, Attention and Action

To investigate how the brain selects the target for an eye movement, multiple stimuli that can be distinguished in some way must be presented. This experimental design is referred to as visual search. The visual search paradigm has been used extensively to investigate visual selection and attention (e.g., Wolfe and Horowitz 2004). In a visual search task, multiple stimuli are presented among which a target is discriminated and located. Search is efficient (with fewer errors and faster response times) if stimuli differ along basic visual feature dimensions, such as color, form or direction of motion. Search becomes less efficient (more errors, longer response times) if the distractors resemble the target or no single feature clearly distinguishes the stimuli. Recently, another approach to investigating the visual and other factors guiding saccade target selection has required participants to locate a more or less vague target embedded in an image of random or structured noise or texture (e.g., Eckstein et al. 2001; Najemnik and Geisler, 2009). A general conclusion drawn from these studies is that humans can direct gaze under these circumstances in a statistically optimal manner. By introducing rapid variation over time in the structure of the image, it is possible to measure the interval of visual input that most effectively guides saccades (e.g., Caspi et al. 2004; Ludwig et al. 2005). These experiments have found that in the ~100 ms before a saccade is initiated, changes of visual input have little or no influence except on subsequent saccades (see also Camalier et al. 2007).

Saccade target selection cannot be discussed without consideration of the allocation of visual attention. In fact, several lines of evidence indicate that visual target selection and the allocation of visual attention may be synonymous. For example, perceptual sensitivity is reduced and saccade latency is elevated if attention is directed away from the target for a saccade (e.g., Kowler et al. 1995; Deubel and Schneider 1996), but this relationship varies with task demands (Deubel 2008). Also, the visual conspicuousness of an oddball stimulus can drive covert (e.g., Theeuwes 1991) and overt (Theeuwes et al. 1998) selection, and non-target elements that resemble a designated target can be inadvertently selected covertly (e.g., Kim and Cave 1995) and overtly (e.g., Zelinsky and Sheinberg 1997; Motter and Belky 1998; Bichot and Schall 1999b). Finally, target selection is influenced by implicit memory representations arising through short-term priming of location or stimulus features for covert (e.g., Maljkovic and Nakayama 1994, 1996) and overt (Bichot and Schall 1999b; McPeek et al. 1999) orienting. These observations are explained most commonly by postulating the existence of a map of salience derived from converging bottom-up and top-down influences (e.g., Itti and Koch 2001; Rodriguez-Sanchez et al. 2007; Wolfe 2007). One major input to the salience map is the maps of the features (color, shape, motion, depth) of elements of the image. Another major input is top-down modulation based on goals and expectations. Peaks of activation in the salience map that develop as a result of competitive interactions represent locations to which attention has become allocated for enhanced visual processing.

Some researchers have suggested that shifts of attention and eye movements are tightly linked (Shepherd et al. 1986; Henderson 1991; Sheliga et al. 1994, 1995; Kowler et al. 1995; Hoffman and Subramaniam 1995; Deubel and Schneider 1996; Hunt and Kingstone 2003). This view is known as the oculomotor readiness hypothesis (Klein 1980; Klein and Pontefract 1994) or the premotor theory of attention (Rizzolatti 1983; Sheliga et al. 1994, 1995). However, the link between directing attention and shifting gaze is not obligatory (Eriksen and Hoffman 1972; Jonides 1980; Posner 1980; Remington 1980; Shepherd et al. 1986; Crawford and Muller 1992; Klein et al. 1992; Reuter-Lorenz and Fendrich 1992). Certainly, when observers scan an image, the timing of saccade production is not under immediate visual control (e.g., Hooge and Erkelens

1996, 1998, 1999; Van Loon et al. 2002). These observations highlight the problem of explaining the timing of saccade production.

We propose that the allocation of attention refers to the manifestation of a particular process or state of the brain during a behavior in the context of alternative stimuli. Accordingly, the allocation of attention across the image need be no more or less than the selective differential activation of neurons in the appropriate network of brain structures. In other words, attention is allocated when and to the extent that the activity of particular neurons represent one as opposed to another location. This measure of the allocation of attention can be distinguished in time and neural process from when, whether and where gaze shifts.

A key measurement in describing stages of processing during eye-movement decisions has been response time, the time taken from visual stimulus onset to saccade. Separating a task into stages of processing allows for experimental manipulation of one stage (e.g., target selection) while holding constant another (e.g., saccade preparation) (Donders 1868; Sternberg 1969; Miller 1988; Schall 2004a). The decision to make a saccade to a target has been described using the principle of accumulation of evidence to a threshold (e.g., Carpenter and Williams 1995; Reddi and Carpenter 2000; Reddi et al. 2003; Smith and Ratcliff 2004). As we shall see later in this chapter, the activity of distinct populations of neurons have been associated with different stages of processing during saccade decisions.

The neural processes described as saccade target selection occur throughout the visual pathway and ocular motor system. Pedagogically, it is easiest to review the experimental evidence for each part of the brain in turn, but the reader should not gain the mistaken impression that the various areas and structures operate in isolation or sequence. In fact, the neural processes responsible for selecting a target and shifting gaze transpire concurrently in an interconnected network woven through the brain from front to back, top to bottom (Figure 1).

Primary Visual Cortex and the Ventral Stream

Selecting a particular element in an image requires that the element be distinguished from others in the image. Such a distinction can be derived from differences in color, shape, motion or depth. Therefore, selection of a target for a visually guided saccade must begin with neural signals that distinguish the features of elements in the image. A cornerstone of visual neuroscience is the fact that neurons in the visual cortex respond selectively according to the color, shape, motion and depth of stimuli. A signal sufficient to distinguish the features of visual objects is available in the first few spikes produced by neurons in primary and extrastriate visual cortex (reviewed by Orban 2008). Selectivity of neural responses for visual features forms the necessary substrate for visual target selection; however, it is not sufficient because targets are distinguished only through a comparison to the features of other stimuli in the image. When more than one stimulus is presented, interactions occur between neurons responding to stimuli in neighboring parts of the scene. Different forms of response modulation by surrounding stimuli has been observed in some neurons primary visual cortex (e.g., Knierim and Van Essen 1992; Zipser et al. 1996; Rossi et al. 2001), areas MT and MST (e.g., Saito et al. 1986) and area V4 (Desimone and Schein 1987). Modulation of the response of neurons to a stimulus in the receptive field by stimuli present in the surrounding region provides the substrate for identifying the location of features that are conspicuously different from surrounding features.

Having larger receptive fields, the responses of neurons in area V4 appear to relate more directly to the guidance of saccades. Neurons in V4 exhibit modulated discharge rates before saccade initiation (Fischer and Boch 1981) that seems to signal enhanced selectivity for the features of the stimulus at the location of the saccade (Moore 1999; Moore and Chang 2008). Also, the receptive fields of V4 neurons have been characterized as reducing in size to effectively focus around the target of the saccade (Tolias et al. 2001), resembling a shift of sensitivity within the receptive field in a spatial attention task (Connor et al. 1997). More direct information about how extrastriate cortex select targets has been obtained in studies that present multiple stimuli. This line of research has been framed by the seminal observation that when two stimuli are presented in the receptive field of many neurons in area V4, the response to the preferred stimulus is modulated according to which of the two stimuli is selected for guiding a behavioral response (reviewed by Reynolds and Chelazzi 2004). For example, several studies have shown that neurons in V4 respond initially indiscriminantly to target and distractor stimuli in their receptive fields but then the activity is modulated to signal through maximal activation the location of the target stimulus, whether it is defined by similarity to a cue stimulus or distinctiveness relative to non-target distractors (Motter 1994a, b; Chelazzi et al. 2001; Ogawa and Komatsu 2004; 2006; Mirabella et al. 2007). The selective activation took some time, on the order of 150 ms, to arise (Figure 1). The time needed to distinguish and locate a target depends on the similarity of the target to non-target objects in the image (e.g., Hayden and Gallant 2005). Nevertheless, this selective activation occurs as well when targets are selected during natural scanning eye movements (Gallant et al. 1998; Mazer and Gallant 2003; Bichot et al. 2005; David et al. 2008).

Measurements of event-related potentials over extrastriate visual cortex of human participants performing tasks that require target selection and attention allocation have identified a signature of the locus and time of attention allocation (e.g., Luck and Hillyard 1994; Woodman and Luck 1999). Referred to as N2pc, it is a slightly more negative polarization arising approximately 200 ms after stimulus presentation in electrodes contralateral as compared to ipsilateral to the attended hemifield. Source localization procedures indicate that the N2pc arises from an early parietal source and a later occipito-temporal source (Hopf et al. 2000). A recent study demonstrated that a homologue of the N2pc can be recorded from electrodes in the surface of the skull in macaque monkeys (Woodman et al. 2007).

The modulation of neural activity that has been observed in, for example, area V4 has also been found in areas in inferior temporal cortex where neural representations of conjunctions of features and of objects arise. The stimulus selectivity of neurons in inferior temporal lobe seems the same during active scanning in a cluttered image as compared to passive presentation (DiCarlo and Maunsell 2000). Studies have described modulation of neurons to attended versus non-attended stimuli (e.g., Richmond and Sato 1987; Sato 1988) and during natural scene viewing and search (Sheinberg and Logothetis 2001; Rolls et al. 2003). The process of selection by modulation of neural activity for target and non-target stimuli that was described for V4 has also been observed in inferior temporal cortex (Chelazzi et al. 1998).

A general conclusion of these studies is that multiple stimuli compete for an explicit neural representation, and the competition among stimuli can be biased by other neural signals that reflect experience or instruction (e.g., Desimone and Duncan 1995). Ultimately, though, enhanced activity in visual cortex represents the features characterizing the target and not that it is a target *per se*. A more general representation of the location of a target regardless of its features is necessary to guide saccadic eye movements. Such a representation has been referred to as a salience map. We will now describe results indicating that neurons instantiating this salience map are present in the superior colliculus as well as areas in the parietal and frontal lobes.

Superior Colliculus

This chapter is focusing on cortical areas, but it should be appreciated that subcortical structures contribute to saccade target selection equally. The most thorough descriptions have been provided for the superior colliculus. These data will lead to the view that certain neurons in the superior colliculus embody a representation of the image that can be identified with a salience map (reviewed by Findlay and Walker 1999; see also Krauzlis et al. 2004) while other neurons contribute to the production of gaze shifts (see Chapter 13 by Munoz).

To learn how the superior colliculus contributes to visual selection processes, many investigators have trained monkeys to identify a target location based on implicit cuing (Goldberg and Wurtz 1972; Wurtz and Mohler 1976a) or by the timing of stimuli or other visual cues (Glimcher and Sparks, 1992; Kustov and Robinson 1996; Basso and Wurtz, 1998; Horwitz and Newsome 2001; Ratcliff et al. 2003; Ignashchenkova et al. 2004; Li and Basso 2005; Port and Wurtz 2009). Of more relevance for our consideration are studies in which multiple stimuli were presented simultaneously, and the target was distinguished from non-target stimuli by properties such as color (Ottes et al. 1987; McPeek and Keller 2002; Shen and Paré 2007; Kim and Basso 2008). While details about the design and the nature or quality of the results for each study vary, the results can be summarized briefly. Initially, when multiple stimuli are presented, activation increases at all locations in the superior colliculus map corresponding to the potential saccade targets. This happens because neurons in the macaque superior colliculus are not naturally selective for visual features like color; however, the neurons can respond to isoluminant chromatic stimuli (White et al. 2009). Following the initial volley, activation becomes relatively lower at locations that would produce saccades to non-target objects and is sustained or grows at locations corresponding to more conspicuous or important potential targets. When the target is easily distinguished from distractors (e.g., a red spot among green spots), then the difference in activity that signals target location arises 100-150 ms after the array appears (Figure 1) and ~50 ms before saccade initiation. Obviously, to contribute to guiding gaze, saccade target selection must occur before saccade initiation, although curiously some authors describe a selection process that follows the saccade (Buschmann and Miller 2007). As we will see, this pattern of activity of neurons in the superior colliculus closely resembles what has been observed in parietal and frontal areas from which these signals may arise through direct cortical afferents or to which these signals may contribute through thalamic relay nuclei.

The visual selection of the target is accomplished by different types of neurons in SC, both those with tonic visual responses and those described as build-up or visuomovement neuons. As will be emphasized in the section describing the frontal eye field below, the selection of the target as a visual location to which to orient attention does inevitably and immediately lead to re-orienting of the eyes.

Recent studies using microstimulation and inactivation have demonstrated a causal role of superior colliculus in target selection (Carello and Krauzlis 2004; McPeek and Keller 2004; McPeek 2008). In one study, reversible inactivation of superior colliculus with lidocaine or muscimol caused deficits in target selection (McPeek and Keller 2004). In this study, monkeys searched for a popout target among three distractors. Before superior colliculus inactivation, monkeys performed with 100% accuracy. After injections, monkeys made saccades to distractors on many trials when the target appeared in the location corresponding to the injection site. This deficit in target selection occurred without deficits in saccade production and occurs when overt orienting is not required among competing stimuli (Lovejoy and Krauzlis 2010), providing further evidence for the dissociation of these processes.

Posterior Parietal Cortex

A great deal is known about parietal cortex contributions to attention and gaze (e.g., Andersen and Buneo 2002; Behrmann et al. 2004; Constantinidis 2006; Gottlieb 2007), and we will only point to studies testing saccade target selection because a more comprehensive account can be found in Chapter 14 (by Paré). Posterior parietal cortex consists of multiple areas; we will focus on results from area 7A and the lateral intraparietal area (LIP).

The importance of LIP in performing visual search is demonstrated by the deficits observed consequent to inactivation of LIP (Wardak et al. 2002, 2004). Recent studies have investigated the responses of neurons in posterior parietal cortex in monkeys confronted with displays consisting of a target and one or more distractors (Platt and Glimcher 1997; Gottlieb et al. 1998; Constantinidis and Steinmetz 2001a, b; Ipata et al. 2006; Thomas and Paré 2007; Balan et al. 2008; Buschman and Miller 2008; Ogawa and Komatsu, 2009). Neurons in area 7a signal the location of a stimulus of one color among distractors of another color (Constantinidis and Steinmetz 2001a). Other studies have examined how neural activity in area LIP participates in target selection (Gottlieb et al. 1998; Ipata et al. 2006; Thomas and Paré 2007; Balan et al. 2008; Buschman and Miller 2008). As observed in the superior colliculus and, as we shall see, the frontal eye field, the initial response to the array did not distinguish the location of the oddball, but when the target was easily distinguished from visual search distractors, then within 100-150 ms the activation increased if the oddball was in the receptive field and decayed if only distractors were in the receptive field (Figure 1). This neural activity is sufficient to represent the location of a conspicuous target. A similar pattern of modulation has been observed in experiments in which monkeys shift gaze to the object in an array of eight distinct objects that matches a sample stimulus. If the object in the receptive field was designated the target, neurons exhibited a significant elevation of activity. When the sample was presented during fixation in the center of the array, the augmented activity for the target arose more than 200 ms after the target was specified. This time is longer than that observed in simple pop-out search because more time was needed to encode the properties of the sample and locate the matching element. The modulation of activity is probably related to the enhancement of responses if it is to be the target for a saccade (e.g., Robinson et al. 1978; Bushnell et al. 1981; Mountcastle et al. 1981) or the attenuation of responses to a stimulus appearing at a location where attention is already allocated (Steinmetz et al. 1994; Robinson et al. 1995; Steinmetz and Constantinidis 1995; Powell and Goldberg 2000).

Overall, current results indicate that the visual representation in posterior parietal cortex represents the location of conspicuous and relevant stimuli, i.e., likely targets for orienting either covertly or overtly. Thus, neurons in posterior parietal cortex embody the properties of units in a salience map (reviewed by Kusunoki et al. 2000; Gottlieb 2007).

Frontal Eye Field

FEF is an area in prefrontal cortex that contributes to transforming visual signals into saccade commands (reviewed by Schall 1997, 2003, 2004b; Schall and Thompson 1999; see also Chapter 15 by Everling). It is well known that microstimulation of FEF elicits saccades to the visual field contralateral to the stimulated hemisphere (e.g., Bruce et al. 1985), mediated by a population of neurons that controls whether and when saccades are initiated (e.g., Bruce and Goldberg 1985; Hanes and Schall 1996; Hanes et al. 1998). These neurons project to superior colliculus (Segraves and Goldberg 1987; Sommer and Wurtz 2000, 2001) and the brainstem

(Segraves 1992), which in turn generate saccades via outputs to the oculomotor nuclei (see Chapter 11 by Cullen). Although traditionally regarded as a motor area, the FEF is equally part of the visual system, being strongly interconnected with numerous visual areas, cortically (e.g., Schall et al. 1995b; Jouve et al. 1998; Barone et al. 2000) and subcortically (e.g., Huerta et al. 1986; Stanton et al. 1988). Most FEF neurons have transient or sustained responses to visual stimuli (Mohler et al. 1973; Bruce and Goldberg 1985; Schall 1991) with relatively fast latencies on the order of 50 ms after the appearance of the stimulus (Schmolesky et al. 1998).

Thus, the clear engagement of FEF in visual and motor processing make it a prime locus in which to investigate the signals involved in visual search and attentional target selection. This approach is validated by the observation that ablation or inactivation of FEF causes specific deficits in producing saccades when distractors are present as in visual search (e.g., Schiller and Chou, 2000; Wardak et al. 2006). In addition, a number of studies in human participants have demonstrated that trans-cranial magnetic stimulation over FEF in a limited timeframe relative to array presentation influences visual search performance, especially when the target is more difficult to locate (Muggleton et al. 2003; O’Shea et al. 2004).

A series of investigations has described specific neural correlates of target selection for visually guided saccades by recording the activity of neurons in the FEF of monkeys trained to shift gaze directly to a target in visual search arrays (Schall and Hanes 1993; Schall et al. 1995a; Thompson et al. 1996; Bichot and Schall 1999a; Sato et al. 2001; Bichot et al. 2001a, b; Murthy et al. 2009; Sato and Schall 2003; Schall 2004b; Schall et al. 2004; Cohen et al. 2009b; see also Ogawa and Komatsu 2006). The extensive evidence for the involvement of FEF in saccade target selection has led to the suggestion that it, like the superior colliculus and parietal cortex, can be understood in terms of a saliency map (reviewed by Thompson et al. 2001; Thompson and Bichot 2005).

Following presentation of an array with a single target among uniform distractors, visually responsive neurons in FEF respond initially indiscriminately to the target or the distractors of the search array in their receptive field. However, before a saccade to the target was generated, a selection process proceeded by which visually responsive neurons in FEF ultimately signaled the location of the oddball target stimulus. If the target of the saccade was in the response field, FEF activity was greatest. If non-target distractors were in the response field, the activity was suppressed. This selection process requires more time when that target is less distinct from the distractors (Sato et al. 2001; Bichot et al. 2001; Cohen et al. 2009b) and occurs if no overt response is made (Thompson et al. 1997) or if target location or property is signaled by through a manual response (Thompson et al. 2005). Furthermore, in monkeys producing sequences of saccades to search for a target embedded in natural scenes FEF neurons signal not only the endpoint of the next saccade but also up to two subsequent saccades (Phillips and Segraves 2010). Clearly, then, the target selection process can be preplanned through a sequence of saccades during natural scanning.

In FEF the target selection process includes spike timing cooperation and competition between pairs of neurons (Cohen et al. 2010). When pairs of neurons with overlapping receptive fields select the target, they cooperate more than when one or neither neuron in the pair selected the target. The amount of cooperation varies with target location, being highest when the target is within both neurons' receptive fields than when it was inside one but not the other, or outside both. This elevation of spike timing coincidences occurred at the time of target selection derived from the modulation of discharge rates. However, correlation in discharge rates of FEF neurons over longer time scales has been reported even before stimulus presentation (Ogawa and

Komatsu, 2010). Neurons with non-overlapping receptive fields exhibited competition through negative spike timing correlations. Thus, perhaps not surprisingly, the neural process of saccade target selection involves dynamic and task-dependent cooperation and competition among neurons.

Further evidence for the network character of the selection process has been obtained in recordings of local field potentials. The target selection process has also been described in local field potentials recorded from FEF (Monosov et al. 2008; Cohen et al. 2009a); in fact the spatially selective activity identifying the location of the target in the visual search array appeared in the spikes ~30 ms before it appeared in the local field potentials. If local field potentials reflect dendritic input and spikes measure neuronal output from a brain region, then this temporal relationship suggests that spatial selection necessary for attention and eye movements is computed locally in FEF from spatially nonselective inputs. When gaze shift errors occur during these visual search tasks, the selection process erroneously guides gaze to a distractor (Thompson et al. 2005), and the errant selection process is evident in the N2pc as well (Heitz et al. 2010). However, when manual response errors occur, the selection process locates the singleton in the search array correctly (Trageser et al. 2008).

Clearly, the visual selection observed in FEF depends on the afferents from the various visual areas conveying feature selectivity. However, FEF also provides extensive feedback connections to extrastriate visual cortex (Schall et al. 1995b; Barone et al. 2000), so the state of neural activity in FEF can influence neural processing in visual cortex. In fact, this connection from FEF to visual cortex is a central feature of models of visual attention (e.g., Hamker and Zirnsak 2006). Several recent studies have described the relationship between activity in FEF and extrastriate cortex. Microstimulation of FEF biases V4 activity in a manner similar to what is observed when attention is allocated (Moore and Armstrong 2003; Armstrong et al. 2006; Armstrong and Moore 2007).

In monkeys trained to maintain fixation and report with a forelimb movement the identity of a visual search target consisting of complex objects, a recent study demonstrated convincingly the contribution of FEF activity to covert spatial attention necessary for target detection and identification (Monosov and Thompson 2009). The location of the target object was cued by the location of a color singleton in an array of rings at each object location. The cues could be valid, invalid or neutral. The magnitude of spatially selective activity signaling the location of the cue prior to the presentation of the search object array was correlated with trends in behavioral performance across valid, invalid, and neutral cue trial conditions. However, the speed and accuracy of target identification on individual trials were predicted by the magnitude of spatially selective activity for the target object and not the spatial cue. Inactivation of FEF produced spatially selective perceptual deficits in the covert search task that were strongest on invalid cue trials that require an endogenous attention shift. Another study performed simultaneous single-unit recordings from FEF and from the region of inferotemporal cortex in which neurons contributed to the object recognition (Monosov et al. 2010). Neural signals specifying target location arose in FEF before neural activity specifying target identity arose in temporal cortex. This sequence is consistent with other evidence that spatial selection precedes and guides formation of complex object representations.

The relationship between FEF and processes in extrastriate visual cortex has also been investigated by comparing the timing of target selection signals in FEF with the N2pc, the signal of target selection measured in an event-related potential over extrastriate cortex (Cohen et al. 2009a). In this study, three signals measuring target selection time were recorded simultaneously while monkeys searched for a target defined by form among distractors: FEF single neurons, FEF local field potentials and ERPs over extrastriate cortex. Single FEF neurons selected the target among distractors first, followed by FEF local field potentials, followed by ERPs (Figure 2). Recent anatomical work suggests that target-selecting neurons in the upper layers of FEF project to V4 (Pouget et al. 2009), providing the major anatomical substrate for the functional signals flowing from FEF to V4.

Evidence that FEF neurons can convey signals related to endogenous spatial attention has been presented recently (Zhou and Thompson 2008). Neurons in FEF exhibit elevated activity when a cue informs monkeys that one of two choice stimuli would appear in their response field. This spatially selective anticipatory activity occurred without any visual stimulus appearing in the neuron’s response field and was not related to motor preparation. These results provide evidence that FEF is a source of a purely top-down spatial attention signal in anticipation of visual stimuli that need to be discriminated.

As noted above, the salience map combines bottom-up information about stimulus properties with top-down information about task goals. This top-down influence can be expressed in many ways. In one experiment monkeys were trained exclusively with search arrays that contained a single item of a constant color among distractor items of another constant color (e.g., red target among green distractors) (Bichot et al. 1996). These monkeys persistently directed gaze to stimuli possessing the learned target color even if the target and distractor colors switched. In monkeys trained exclusively on targets of one color, about half of FEF neurons show selective responses for stimuli of that color appearing in the earliest spikes. This result indicates that the visual system can be configured to provide preferential processing of selected stimuli.

In another experiment monkeys were trained to perform visual search for a conjunction of features (such as a red cross among red circles, green crosses and green circles); this requires an explicit memory representation to identify the target (e.g., Treisman and Sato 1990). Monkeys’ performance and the neural selection process in FEF exhibited two, separate contextual influences: visual similarity of distractors to the target and the history of target properties (Bichot and Schall 1999a, b). The evidence for the influence of visual similarity was revealed by the pattern of occasional erroneous saccades during conjunction search. Erroneous saccades tended to direct gaze to distractors that resembled the current target. Similar observations have been made with human observers during covert (Kim and Cave 1995) and overt orienting (Findlay 1997; Motter and Belky 1998). Now, when monkeys successfully shifted gaze to the target, following the initial indiscriminate response, FEF neurons not only discriminated the target from distractors but also discriminated among the non-selected distractors. More activation was present for distractors that were the same shape or color as the target than for a distractor that shared neither feature of the target. One consequence of this observation is that stimuli that are not selected overtly may still influence subsequent processing because of the differential neural representation. The history of stimulus presentation across sessions also affected the selection process during conjunction search. If an error was made, monkeys showed a significant tendency (in addition to the visual similarity tendency just described) to shift gaze to the distractors that had been the target in the previous session. Recordings from FEF neurons during trials with correct saccades to the conjunction target revealed a corresponding discrimination among distractors with more activation for distractors that had been the target during the previous session. This effect was evident across sessions that were more than a day apart and persisted throughout experimental sessions.

Another expression of cognitive control of visual search is expressed on a shorter time scale. Humans and monkeys are affected by trial-to-trial changes in stimulus features and target location during pop-out visual search. For example, repetition of stimulus features improves performance. This feature-based facilitation of return was manifested in the target discrimination process in FEF; neurons discriminated the target from distractors earlier and better with repetition of stimulus features, corresponding to improvements in saccade latency and accuracy, respectively. In contrast to the repetition of features, repetition of target position increased saccade latency. This location-based inhibition of return was reflected in the neuronal discrimination process but not in the baseline activity in FEF. These results show adjustments of the target selection process in FEF contributing to changes in performance across trials due to sequential regularities in display properties.

A major question in this line of research concerns the relationship of the visual target selection process to saccade preparation and production. This question touches on multiple major questions. First, what is the origin of the variability of fixation duration between saccades made during scanning a scene or reading. Multiple studies have found that the time spent fixating elements of an image cannot be explained just by the properties of the image (e.g., Jacobs 1987; Hooge and Erkelens 1996); however, more recent work has provided evidence for immediate control of some fixation periods (Henderson and Graham 2008). In general, fixation duration seems to be adjusted according to the difficulty of finding the desired target, but moment-by-moment control of fixation duration based on the properties of the image does not seem to occur. This observation indicates that a form of executive control can be exerted on saccade production. Second, the relation of target selection and associated attention allocation with saccade production has been the focus of the oculomotor readiness or premotor theory of attention. Neurophysiological and anatomical data have been obtained that address specific claims of this theory. Finally, understanding how target selection leads to adaptive saccade production is an instance of the more general problem of understanding the mechanisms responsible for response times. A marriage of neurophysiological measurements and mental chronometry has provided new insights supporting the theory that response times are the outcome of successive, stochastic stages of processing.

The neural process of target selection occupies a certain amount of time that can be measured with reasonable accuracy. This provides an opportunity to determine how the time of visual target selection relates to the time of saccade initiation. This work is motivated by the general hypothesis that behavioral response times are occupied by more or less distinct stages of processing (Donders 1868; Sternberg 1969; Miller 1988; Schall 2004a). Recent studies have investigated how the time taken to select a target relates to the time taken to initiate the saccade.

One approach to this is the well-known method of selective influence. Different stages of processing should be influenced by different manipulations. The time of target selection by FEF neurons depends on the quality of the stimuli and, as described above, the cognitive context. When the discrimination of the target is easy because the target is visually distinct from the distractors, then the time taken by neurons in FEF to locate the target is relatively short (~140 ms for pop-out displays) and on average does not account for the variability and duration of saccade latency (Figure 3A)[1]. When the discrimination of the target is more difficult because the target

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[1] Studies of LIP (Ipata et al. 2006; Thomas and Paré 2007) have not found this relationship. These investigators found that the time of target selection by LIP neurons was more correlated with response time. One possible account for this difference is the behavioral requirements in the respective experiments. In all of the experiments in our laboratory monkeys are required to produce a single saccade to the target; this emphasizes accuracy. In the

more closely resembles the distractors, then the time taken by neurons in FEF to locate the target increases and accounts for a larger fraction but not all of the variability and duration of saccade latency (Bichot et al. 2001a; Sato et al. 2001; Cohen et al. 2009b). For example, in monkeys performing a search for a T (or L) among randomly oriented L's (or T's) with arrays of 2, 4 or 8 elements, the time taken for FEF neurons to locate the target increases with the number of objects in the array. However, even in the most difficult search in the 8 object array, saccades were initiated well after the target was selected.

If the time of visual target selection during search does not account for the full duration and variability of saccade initiation times, then some other process must occur to prepare and produce the saccade. As described above, a population of neurons in FEF and superior colliculus linked through the basal ganglia and thalamus provides the input to the brainstem network that produces the saccade. The activation of these neurons in FEF corresponds to the process of saccade preparation with the activation of these presaccadic movement neurons (also referred to as build-up, prelude or long-lead burst neurons). Saccades are initiated when the level of activation in this network reaches a certain level that may vary across task conditions but appears to be constant within a condition (Hanes and Schall 1996; Dorris et al. 1997; Fecteau and Munoz 2007; Woodman et al. 2008) (Figure 3B). Most of the variability of the latencies of saccades to a visual target can be accounted for by randomness in the rate of growth of activity to the threshold (Hanes and Schall 1996), although other studies in other task conditions find variability of the baseline activity as well (Dorris et al. 1997; Fecteau and Munoz 2007). When saccade latencies are delayed because the target selection process takes longer, this is accomplished by a delay in the time when the activity begins to accumulate (Woodman et al. 2008).

A recent model was developed to investigate how the signals from the visual selection neurons can be transformed into a saccade command (Purcell et al. 2010). The model consists of a network of deterministic units that integrate through time the actual physiological signals recorded from ensembles of tonic visual neurons in FEF that select the target during visual search. Response times were specified by the time at which the integrated signal reached a threshold. The model explored the role of leak in the integration process and of feedforward and lateral inhibition by determining model parameters that provided the best fit to the actual distributions of response times and produced activation profiles that quantitatively corresponded to the form of actual movement neuron activity. To account for both behavioral and neural data, it was found that the model must include another form of inhibition that gates the flow of perceptual evidence to the accumulator.

Thus, the picture that emerges is that the process of visual selection occupies a certain amount of time that can be shorter and less variable if the target is conspicuous, or it can be longer and more variable if the target is less conspicuous. If subjects wish to prevent a saccade to a non-target stimulus, then the preparation of the saccade can be delayed until the visual selection process has proceeded to a high degree of resolution. Neural activity mediating saccade preparation begins to grow as the selection process is completed and (for reasons that are not clear) the rate of growth of activity leading to the movement varies apparently randomly such that sometimes gaze shifts sooner and sometimes gaze shifts later. Systematic adjustments of saccade latency, though, appear to arise through changes in the time that the accumulation of activity begins. In fact, further evidence for the distinction between target selection and saccade

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experiments on LIP monkeys were permitted to produce multiple saccades to locate the target; this allows a strategy of speed over accuracy of the saccade. Experimental verification of this possibility has not been obtained to date.

preparation is the observation that the movement neurons in FEF do not discharge at all above baseline when monkeys maintain fixation when monkeys report target location through a manual response (Thompson et al. 2005).

On the other hand, occasionally it is possible for the saccade preparation process to become activated before identification of the currently fixated element and selection of the next target are completed. For example, during visual search neurons in FEF with no visual response and only presaccadic movement activity can exhibit partial activation for non-target stimuli that resemble the target (Bichot et al. 2001b). Such activation of movement neurons can, if excessive, result in premature, erroneous saccades. Independence of visual selection and response preparation is also necessary to explain the production of saccades that are not directed to the location of the selected target.

The dynamics of visual selection and saccade preparation by the frontal eye field has been investigated in macaque monkeys performing a search-step task that combines the classic double-step saccade task with visual search (Camalier et al. 2007). In most trials the target appeared in an array of distractors and reward was earned for producing a saccade to the target. On random trials before the saccade was initiated, the target and one distractor swapped locations, and monkeys were rewarded for shifting gaze to the new target location. Performance of this task is unpredictable, but on average, the longer the delay of the target step, the less likely will monkeys (or humans) correctly shift gaze to the new target location. If target selection and saccade preparation are too far advanced before the target step, then they will shift gaze to the old target location. These errors are commonly followed by corrective saccades to the new target location. Now, some investigators use double-step target presentation as an explicit means of dissociating retinal error from motor error, but performance of this task under the instruction to follow the target steps is different from performance under the instruction to redirect gaze to the final target location (Ray et al. 2004).

Performance of this task can be accounted for as the outcome of a race between processes producing the two saccades and a process that inhibits production of the first saccades (Camalier et al. 2007). The race model provides a powerful framework in which to interpret and understand the activity of the different types of neurons. Central to this model is the duration of the process that interrupts preparation of the first saccade on trials when the target steps. This interval is referred to as *target step reaction time*. The physiological properties of neurons in FEF of monkeys performing this task have been described in several papers (Murthy et al. 2007, 2009). When the target stepped out of a movement field, noncompensated saccades to the original target location were produced when movement-related activity grew rapidly to a threshold. Compensated saccades to the final target location were produced when the growth of the original movement-related activity was interrupted within target step reaction time and was replaced by activation of other neurons producing the compensated saccade. When the target stepped into a receptive field, visual neurons selected the new target location regardless of the monkeys’ response. In other words, even when gaze shifted away from the pop-out oddball of a search array, visual neurons in FEF represented the current location of the target. A modulation of this form has also been described in the superior colliculus (McPeek and Keller, 2002). When the target stepped out of a receptive field most visual neurons maintained the representation of the original target location, but a minority of visual neurons showed reduced activity. These findings indicate that visual activity in the frontal eye field signals the location of targets for orienting while movement-related activity instantiates saccade preparation.

During natural scanning eye movements one observes occasional instances of saccades initiated after fixation intervals that are too short to permit visual analysis of the image sufficient to guide gaze. In the double-step or search-step task corrective saccades are observed following similarly short fixation of the original target location (Becker and Jürgens, 1979; Camalier et al. 2007; Sharika et al. 2008). In fact, the race model provides an explanation for the incidence and timing of these corrective saccades that includes an account of why midflight corrections are rare. 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 many neurons began before visual feedback of the error was registered and that of a few neurons began before the error saccade was completed (Murthy et al. 2007; see also Phillips and Segraves 2010). Corrective saccade can be produced, though, only if other neurons in the brain have located the new target location and maintain that representation through the production of the error. As noted above, this is just what the visual neurons in FEF do. However, this selection process is itself a variable process that may be more or less complete at the time of saccade initiation. Thus, incomplete suppression of distractor-related activity results in curvature of saccades toward the distractor (McPeek 2006; see also McPeek et al. 2003).

The double-step or search-step condition dissociates visual target location from saccade endpoint incidentally. The dissociation can also be accomplished explicitly through instruction. For example, it is possible to shift gaze in the direction opposite a visual target, referred to as antisaccade. In monkeys producing antisaccades visually responsive neurons in the superior colliculus and FEF respond if the target falls in the receptive field, and movement neurons are active for saccades into the movement field whether it is a prosaccade or an antisaccade (Everling et al. 1999; Everling and Munoz 2000). To investigate the relationship of visual target selection to saccade preparation explicitly, monkeys were trained to make a prosaccade to a color singleton or an antisaccade to the distractor located opposite the singleton; the shape of the singleton cued the direction of the saccade (Sato and Schall 2003; Schall 2004). As observed in previous studies, the response time for antisaccades was greater than that for prosaccades. A goal of this experiment was to account for this difference in terms of the neural processes that locate the singleton, encode its shape, map the stimulus onto the response, select the endpoint of the saccade and finally initiate the saccade. Two types of visually-responseive neurons could be distinguished in FEF. The first, called Type I, exhibited the typical pattern of initially indiscriminant activity followed by selection of the singleton in the response field through elevated discharge rate regardless of whether the singleton's features cue a prosaccade or an anti saccade. Some of these Type I neurons maintained the representation of singleton location in antisaccade trials until the saccade was produced. However, the majority of the Type I neurons exhibited a remarkable and dramatic modulation of discharge rate before the antisaccade wsa initiated (Figure 4A). After showing higher discharge rates for the singleton as compared to a distractor in the receptive field, the firing rates changed such that higher discharge rates were observed for the endpoint of the antisaccade relative to the singleton location. This modulation could be described as the focus of attention shifting from one location to the other before the saccade. The second type of neuron, called Type II, resembled qualitatively the form of modulation of Type I neurons in prosaccade trials, but in antisaccade trials, these neurons did not select the location of the singleton and only selected the endpoint of the saccade (Figure 4B). This endpoint selection was distinct from movement neuron activation, but the selection times of Type II, but not Type I, neurons accounted from some of the variability of saccade response time on prosaccade or antisaccade trials.

This experiment revealed a sequence of processes that can be distinguished in the modulation of different populations of neurons in FEF. The timecourse of these processes can be measured and compared across stimulus-reponse mapping rules (Figure 4C). More details about the relationship of singleton selection time, endpoint selection time and response time are described in Sato and Schall (2003). To summarize, Type I neurons selected the singleton earlier than did Type II neurons. In the population of Type I neurons the time of selection of the singleton in prosaccade and antisaccade trials did not vary with stimulus response mapping or account for the difference in RT. However, the singleton selection time of Type II neurons in prosaccade trials was less synchronized with array presentation and more related to the time of saccade initiation. In antisaccade trials the time of endpoint selection by Type I neurons was significantly later than that of Type II neurons. This result is as if the endpoint of a saccade must be identified before attention can shift to the location. The endpoint selection time of Type I neurons in antisaccade trials was too late to explain the increase in RT relative to prosaccade trials. In contrast, the endpoint selection time of Type II neurons in antisaccade trials, like the singleton selection time in prosaccade trials, accounted for some but not all of the delay and variability of RT.

This visual search task with prosaccades and antisaccades provided a powerful test of the pemotor theory of attention (Juan et al. 2004). The premotor theory of attention states that shifting visual spatial attention corresponds to preparing a saccade. The focus of attention was dissociated momentarily from the endpoint of a saccade by training monkeys to perform visual search for an attention-capturing color singleton and then shift gaze either toward (prosaccade) or opposite (antisaccade) this color singleton according to its orientation. 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. Eye movements evoked on prosaccade trials deviated progressively toward the singleton that was the endpoint of the saccade. Eye movements evoked on antisaccade trials deviated not toward the singleton but only toward the saccade endpoint opposite the singleton. These results are interpreted in relation to previous work showing that on antisaccade trials most visually responsive neurons in frontal eye field initially select the singleton while attention is allocated to distinguish its shape. In contrast, preliminary data indicates that movement neurons are activated but do not produce a directional signal after the saccade endpoint is selected. Evidence consistent with these observations has been obtained in a study of human participants using transcranial magnetic stimulation (Juan et al. 2008), and in a study probing explicitly the locus of attention (Smith and Schenk 2007). Thus, the brain can covertly orient attention without preparing a saccade to the locus of attention. The premotor theory should be revised to accommodate these results.

To produce arbitrary responses to specific stimuli requires a mechanism to encode the rules and context of the task. This brings us to areas in prefrontal cortex rostral to the FEF.

Prefrontal Cortex

Rostral to the FEF are areas of ventrolateral and dorsolateral prefrontal cortex that have been the focus of extensive investigation and theory (e.g., Fuster 2008). Before proceeding, we should note that the FEF is certainly an area in prefrontal cortex defined by the presence of a granular layer and afferents from the mediodorsal nucleus of the thalamus. Nevertheless, to simplify and summarize the function of the more rostral areas, we can state that they contribute to enacting flexible stimulus-response rules through time. According to the hypothesis that attentional selection and saccade production are accomplished by different neural circuits, then dorsolateral prefrontal cortex could enact this flexibility by modulating either the salience map represented by the visually responsive neurons or by modulating the timing of the saccade preparation process. Clear evidence for task-related modulation of the target selection process has been obtained in FEF (e.g., Bichot and Schall 1999; 2002). Equally clear evidence for task-related modulation of the timing of saccade preparation process has also been obtained in FEF (Woodman et al. 2007). Further research is needed to understand how the flexible representations afforded by prefrontal cortex influence saccade target selection.

Recent lesion and microstimulation studies have established a general role of macaque dorsolateral prefrontal cortex in attention and saccade target selection (Opris et al. 2005; Rossi et al. 2007). However, we must note that the conditions of the experiments investigating prefrontal cortex were not typical of the visual search experiments reviewed above. For example, in one study, monkeys discriminated the orientation of a colored target grating among distractor gratings. When the cue indicating which stimulus was the target was held constant across trials, monkeys with prefrontal cortex lesions were unimpared. When the cue switched frequently across trials, however, monkeys with prefrontal cortex lesions were severely impaired in attending to the target.

The activity of neurons in prefrontal cortex areas rostral to FEF has been described during tasks that required different forms of visual target selection (Boussaoud and Wise 1993; Rainer et al. 1998; Ferrera et al. 1999; Kim and Shadlen 1999; Hasegawa et al. 2000; Constantinidis et al. 2001; Everling et al. 2006; Buschman and Miller 2007). In some of these studies the selection of the target appeared as effectively an all-or-none activation, largely because the responses began after the selection process was completed in visual areas of the cortex.

A common feature of neurons recorded in dorsolateral prefrontal cortex is the presence of activity during enforced delay periods in which monkeys must remember specific aspects of the stimuli to guide the eventual response. The characteristics of this delay period activation have been described in numerous studies. For example, one study presented monkeys with two stimuli, a bright target and a distractor with brightness that was varied across trials from that of the dim background to that of the bright target (Constantinidis et al. 2001). In this way the discriminability of the target from the distractor was varied. After an instructed delay in which the stimuli had been removed, monkeys shifted gaze to the location occupied by the brighter stimulus. The activation during the delay period varied according to the brightness of the stimulus in the receptive field and the performance of the monkeys. Neurons remained active during the delay period even if the stimulus in the receptive field had been the distractor. This affords an opportunity for the properties of the non-selected stimuli to influence subsequent performance. Also, the magnitude of the activation varied such that if the distractor was more similar to the target, the activation evoked by the distractor was more similar to the activation evoked by the target.

To summarize, the studies of dorsolateral prefrontal cortex have indicated that neurons may not participate directly in the target selection process but can encode the properties of selected and non-selected stimuli. Further work is needed to discover how the function of dorsolateral prefrontal cortex influences target selection in the more caudal parts of the brain.

Summary

Vision occurs naturally in a continuous cycle of fixations interrupted by gaze shifts. The guidance of these eye movements requires information about what is where in the image. The identity of objects is derived mainly from their visible features. Single neurons in the visual pathway represent the presence of specific features by the level of activation. Each point in the visual field is represented by populations of neurons activated by all types of features. Topographic representations are found throughout the visual and oculomotor systems; neighboring neurons tend to represent similar visual field locations or saccades.

When confronted by an image with many possible targets, the visual system compares the features of elements across the visual field. The retinotopic maps of the visual field facilitate local interactions to implement such comparisons; in particular, a network of lateral inhibition can extract the locations of the most conspicuous stimuli in the visual field. The process of these comparisons can be influenced by knowledge so that inconspicuous but important elements in the image can be the focus of gaze. This selection process results in a state of activation in which neurons with potential targets in their receptive field are more active, and neurons with non-targets in their receptive field are less active.

The outcome of this selection process can be represented at a level of abstraction distinct from the representation of the features themselves. This is why the hypothetical construct of a salience map is useful. The state of neural selection of a salient target relative to surrounding non-target elements amounts to the covert allocation of attention that usually precedes overt shifts of gaze. The time taken for the brain to achieve an explicit representation of the location of a target varies predictably according to how distinct the target appears in relation to non-target elements.

Coordinated with this visual processing is activation in a network including FEF and superior colliculus that is responsible for producing the eye movement. A saccade is produced when the activation at one location within the motor map reaches a critical threshold. One job of visual processing influenced by memory and goals, is to insure that only one site – the best site – within the map of movements becomes activated. This is done when the neurons signaling the location of the desired target develop enhanced activation while the neurons responding to other locations are attenuated. When confronted with ambiguous images having multiple potential targets, partial activation can occur in parts of the motor map representing saccades to non-target elements that resemble the target. Saccade target selection converts an initially ambiguous pattern of neural activation into a pattern that reliably signals one target location in a winner-take-all fashion. However, the representation of likely targets for orienting does not automatically and unalterably produce a saccade. Sometimes potential targets are perceived without an overt gaze shift or gaze can shift to locations not occupied by salient stimuli. The explanation of this flexible coupling between target selection and saccade production requires separate stages or modules that select a target for orienting and that produce gaze shifts. The flexible relationship between target selection and saccade production also affords the ability to emphasize speed or accuracy. Accuracy in fixating correctly can be emphasized at the expense of speed by allowing the visual selection process to resolve alternatives before producing a saccade. On the other hand, accuracy can be sacrificed for speed, allowing the visuomotor system to produce a saccade that may be inaccurate because it is premature relative to the target selection process.

Obviously, many questions remain, but looking back just 20 years it is gratifying to note the progress that has been made describing how the brain selects the targets for saccades.

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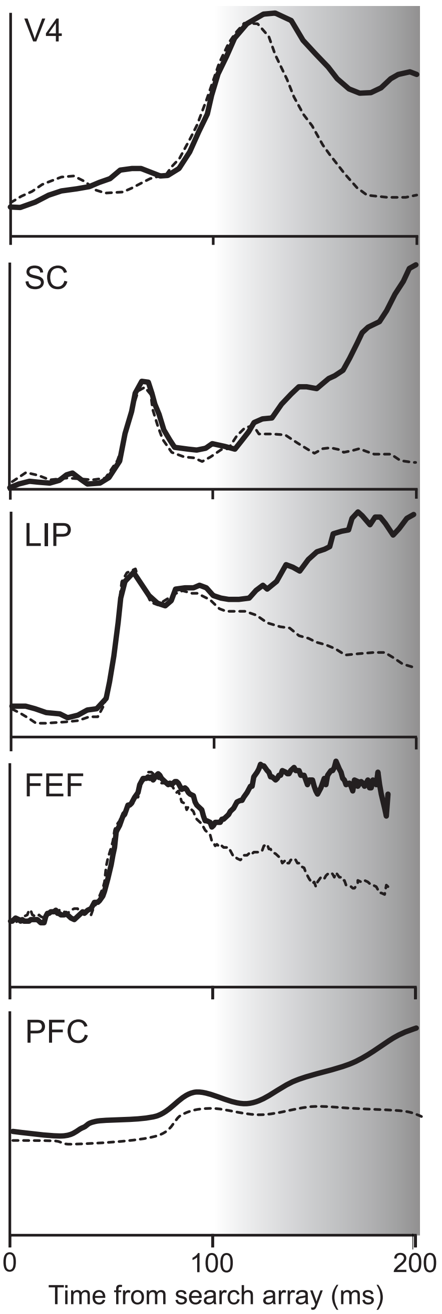
FIGURE LEGENDS

FIGURE 1 Illustration of visual and saccade target selection of representative single neurons in area V4 (adapted from Ogawa and Komatsu 2004), superior colliculus (SC) (adapted from McPeek and Keller 2002), area LIP (adapted from Thomas and Paré 2007), FEF (adapted from Thompson et al. 1996) and area 46 of prefrontal cortex (adapted from Hasegawa et al. 2000). The average discharge rate on trials when the target appeared in the response field (thick line) is plotted with the average discharge rate on trials when distractors appeared in the response field, and the targe was elsewhere (thin dashed line). Although the data were collected in different areas and under different stimulus and task conditions, it is clear that a concurrent process of target selection occurs throughout the network.

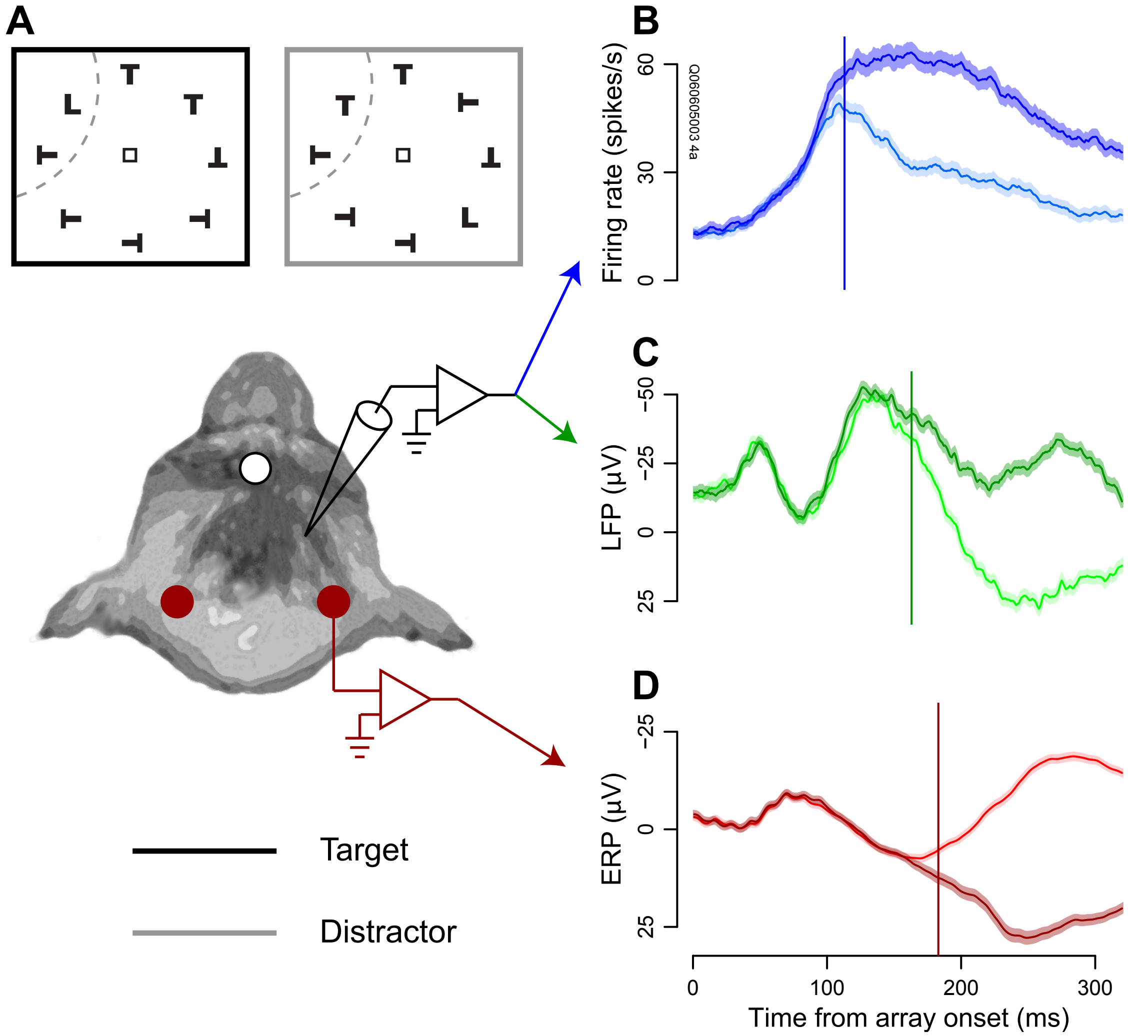
FIGURE 2 Target selection during a representative session. (A) Top - visual search display (shown here with a set size of 8) with the target (L) inside the neuron's receptive field (indicated by the dashed arc) (left) and opposite the receptive field (right). Monkeys searched for a T or L target among 1, 3 or 7 L or T distractors. Bottom - schematic of recording sites and signals. Single unit discharges (blue) and local field potentials (green) were recorded intracranially from the frontal eye field. Event-related potentials were recorded from electrodes over extrastriate visual cortex (red). (B) Average activity of one neuron when the search target was inside (dark) and opposite (light) its receptive field. Bands around average firing rates show time-varying standard error of the mean. Vertical line indicates target selection time when the two curves became statistically significantly different. (C) FEF LFP with the target inside (dark) and opposite (light) the simultaneously recorded neuron's receptive field. (D) ERP over extrastriate visual cortex from trials with the target inside (dark) and opposite (light) the receptive field of the concomitantly recorded FEF neuron. This component is the macaque homologue of the human N2pc (m-N2pc). (from Cohen et al. 2009).

FIGURE 3 Relation of time of neural target selection to time of saccade initiation during efficient search for a green target among red distractors. The activity of an FEF neuron representing the target (thick) or distractors (thin) is shown during trials with saccades of the shortest (top) or longest (bottom) latencies. The upper plots in each panel indicates the distribution of saccade latencies with the range selected for the analysis of activity shaded. The time at which the activity distinguished whether a target or distractor was in the receptive field is marked by the dashed vertical line. The neuron discriminated the target from distractors following a relatively constant interval after presentation of the search array. Modified from Sato et al. (2001).

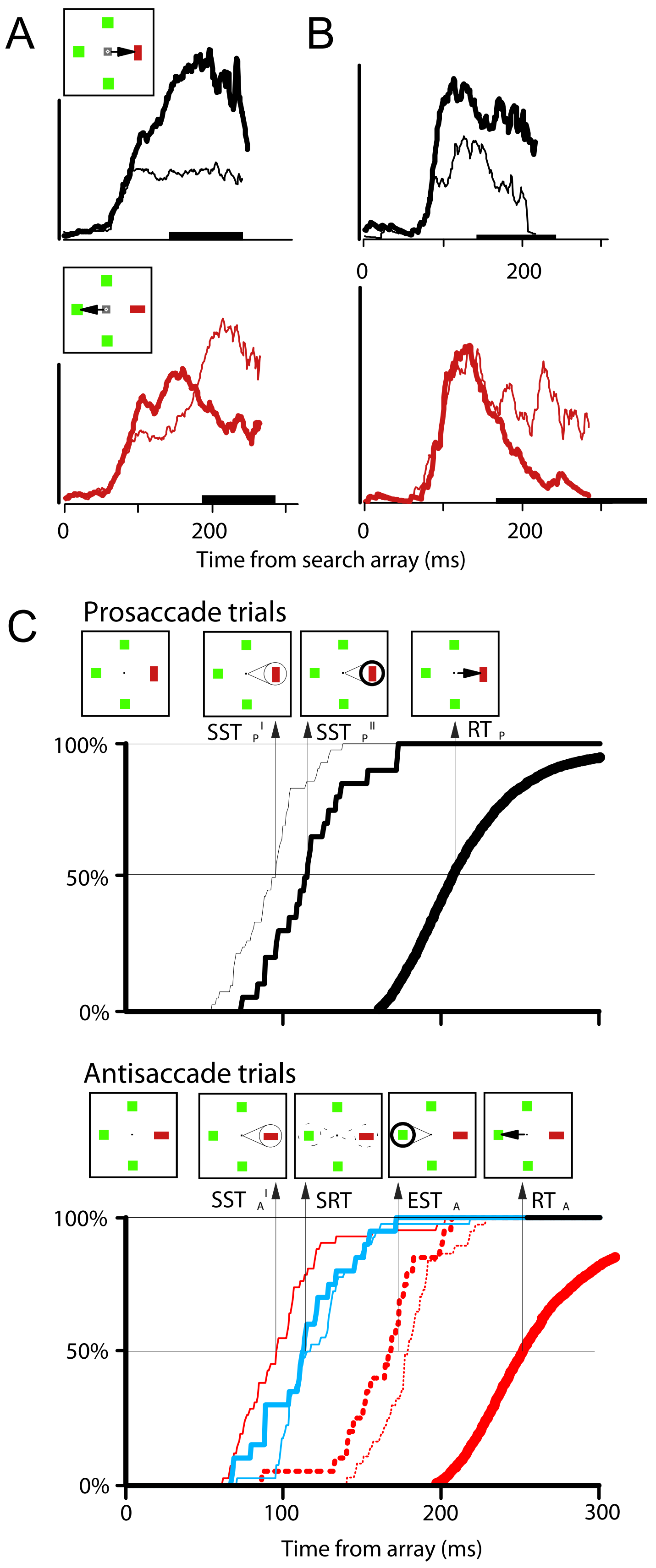
FIGURE 4 Pattern and timing of neural activity in FEF when mapping between location of visual target and endpoint of saccade is varied. (A) Activity of FEF neuron with activity that can be identified with the allocation of attention (Type I). Average spike density function when the singleton fell in the neuron's receptive field (thick line) and when the singleton was located opposite the receptive field (thin line) in prosaccade (top) and antisaccade (bottom) trials. Bracket on abscissa marks range of RT. Scale bar represents 100 spikes/sec. (B) Activity of FEF neuron with activity that can be identified with selection of the saccade endpoint (Type II). (C) Cumulative distributions of modulation times in prosaccade (top) and antisaccade (bottom) trials for Type I (thin) and Type II (thicker) neurons with corresponding RT (thickest). The inset arrays indicate hypothesized functional correlates. After presentation of the array, selection of the singleton location occurs at the SST of Type I neurons (indicated by the spotlight on the singleton); this occurs at the same time in prosaccade and antisaccade trials and does not relate to whether or when gaze shifts. In prosaccade but not antisaccade trials Type II neurons select the singleton at a later time which accounts for some of the variability of RT. A comparison of activation in prosaccade and antisaccade trials reveals the time at which the shape of the singleton is encoded to specify the correct saccade direction; this follows singleton selection and coincides for Type I (thin blue) and Type II (thicker blue) neurons in antisaccade trials. At the moment marked by SRT in antisaccade trials the representation of the singleton decreases, and the representation of the location opposite the singleton, the endpoint of the antisaccade increases (indicated by the weaker spotlight on the singleton and growing spotlight on the saccade endpoint). At this same time in prosaccade trials the representation of the saccade endpoint is enhanced by the selection that occurs in the Type II neurons (indicated by the highlighted spotlight on the singleton). Subsequently, in antisaccade trials the endpoint of the saccade becomes selected more than the location of the singleton by Type I (thin, red, dashed) and Type II (thicker red, dashed) neurons (indicated by the highlighted spotlight on the antisaccade endpoint). The time taken to select the endpoint of the saccade predicts some of the delay and variability of RT. Modified from Sato and Schall (2003)



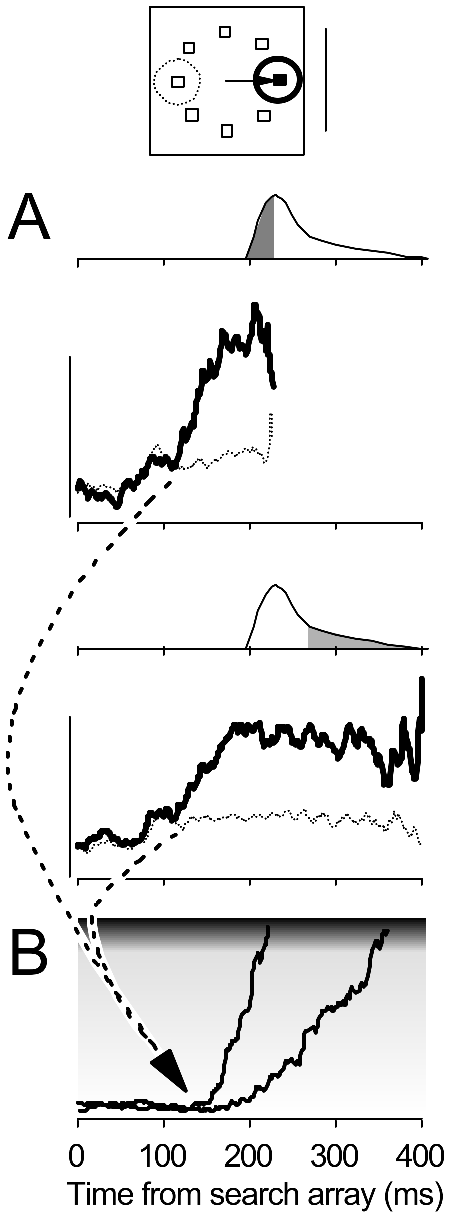
Schall & Cohen, Figure 1



Schall & Cohen, Figure 2



Schall & Cohen, Figure 3



Schall & Cohen, Figure 4