63 Selection of Targets for Saccadic Eye Movements: An Update

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Vision is an active process. Because primate vision is acute only at the fovea, gaze must shift to identify objects in the scene. However, vision is dramatically impaired during rapid gaze shifts. Therefore, the visual and ocular motor systems must be coordinated judiciously. Because gaze can be directed to only one item at a time, some process must distinguish among possible locations to select the target for a saccade. The outcome of the selection process is defined by the goals of visually guided behavior. Analyses of the pattern of eye movements have revealed regularities such as concentrating on conspicuous and informative features of an image during scrutiny of simple geometric stimuli (Liversedge & Findlay, 2000), natural images (Henderson, 2011) or text (Rayner & Liversedge, 2011), leading to the view that we can direct gaze in a statistically optimal manner (Najemnik & Geisler, 2009). Saccade target selection is coordinated with movements of other parts of the body during natural behaviors (Hayhoe & Ballard, 2011; Land & Tatler, 2009). Research focused on the neural mechanisms of visual search and saccade target selection began 20 years ago (Schall & Hanes, 1993) and is now undertaken by many research groups. This topic has been reviewed thoroughly both in the previous edition of this book (Schall, 2004) and in subsequent publications (Bichot & Desimone, 2006; Bisley & Goldberg, 2010; Constantinidis, 2006; Gottlieb & Balan, 2010; Paré & Dorris, 2011; Schall & Cohen, 2011; Schiller & Tehovnik, 2005; Wardak, Olivier, & Duhamel, 2011), so this chapter will orient the reader to the general issues, highlight more recent findings, and frame the major remaining questions. The citations will be selective and recent; the interested student can find classic references in the previous version of this chapter.

VISUAL SEARCH: SALIENCE, ATTENTION, AND STAGES OF PROCESSING

To investigate how the brain selects the target for an eye movement, multiple stimuli that can be distinguished in some way must be presented. Referred to as visual search, this experimental design has been used extensively to investigate visual selection and attention (reviewed by Geisler & Cormack, 2011; Wolfe & Horowitz, 2004). 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. In contrast, if the distractors resemble the target or no single feature clearly distinguishes the stimuli, then search becomes less efficient (more errors, longer response times).

These observations have been explained most commonly by postulating the existence of a map of salience[1] derived from converging bottom-up and top-down influences (Bundesen, Habekost, & Kyllingsbaek, 2011; Tsotsos, 2011). Salience refers to how distinct one element of the image is from surrounding elements. This distinctness can occur because the element has visual features that are very different from the surroundings (a ripe, red berry in green leaves). The distinctness can also occur because the element is more important than others (the face of a friend among strangers). The distinctness derived from visual features and importance confers upon that part of the image greater likelihood of receiving enhanced visual processing and a gaze shift. In the models of visual search referred to above, 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. The representation of likely targets that is implicit in and dependent on the feature maps becomes explicit in the salience map. Peaks of activation in the salience map that develop as a result of competitive interactions represent locations that have been selected for further processing and thus covert orienting of attention.

Saccade target selection coincides with the allocation of visual attention that has been the focus of considerable research (e.g., chapters 23, 24, 71, 75, 76–78). Attentional allocation and saccade production interact in various ways. Some investigators have explained the connection between saccade production and attention

allocation by proposing that the allocation of attention amounts to a subthreshold command to shift gaze. This view is known as the oculomotor readiness hypothesis (Klein, 1980) or the premotor theory of attention (Rizzolatti, 1983). Although an influential guiding hypothesis, numerous observations are inconsistent with a strict interpretation of this hypothesis (reviewed by Awh, Armstrong, & Moore, 2006), and I will review more below. Indeed, I will emphasize the very basic fact that the focus of visual attention can be directed away from the focus of gaze showing that the link between shifting gaze and directing attention is not obligatory. Various lines of evidence demonstrate that the neural process of selecting a target for orienting is functionally distinct from the neural process of preparing a saccade. This distinction has been confirmed by experimental manipulations that independently influence the distinct and successive stages (Sternberg, 2011).

OVERVIEW OF NEURAL SUBSTRATES

As readers of this volume know, saccades are ultimately produced by a network of neurons in the brainstem (chapters 60, 61; see also Cullen & Van Horn 2011). This network that shapes the pattern of activation of the motor neurons innervating extraocular muscles requires two inputs—where to shift gaze and when to initiate the movement. Key brain structures controlling the initiation of saccades by the brainstem include the superior colliculus (SC) (chapter 64; see also White & Munoz, 2011b) and the frontal eye field (FEF; Johnston & Everling, 2011; Schall & Boucher, 2007) operating in a recurrent network through the basal ganglia (Vokoun, Mahamed, & Basso, 2011) and thalamus (Tanaka & Kunimatsu, 2011). Saccade endpoints are specified by the spatial pattern of activation in these structures, which can be appreciated most clearly in the SC (see figure 63.1). Presaccadic neurons that lead to initiation of saccades have movement fields wherein they are most active before saccades of a particular direction and amplitude and progressively less active before saccades deviating from the optimal. Thus, before each saccade, neurons over a rather broad extent of SC are activated in a graded manner. The space of saccade direction and amplitude is mapped in a topographic fashion corresponding to the map of visual space in the superficial layers of the SC. To produce a signal leading to a saccade of a particular direction and amplitude, the activation of many cells in a region of the motor map are combined as vectors. Through this vector combination saccadic endpoints can be more precise than the size of individual neuron movement fields.

Evidence for the vector combination hypothesis is obtained either by electrically stimulating two points in the SC or FEF (Robinson, 1972) or by presenting a pair of visual targets close together (Findlay, 1982). This results in a larger zone of activation occurring across the map (see figure 63.1B). A saccade resulting from the vector average of the zone of activation directs gaze to a location between the targets. The problem of saccade target selection is highlighted, though, when a circular array of stimuli is presented, resulting in a spatial distribution of activation in the SC with multiple peaks that are balanced around the map (see figure 63.1C). The vector combination of this distribution of activity amounts to a resultant of no net length—not a very useful outcome. To produce a useful saccade, the activation in the map of the SC and associated structures must be limited to the neurons contributing to generating just that saccade. Thus, if more than one location in the SC map becomes activated, then additional processing must resolve which of the peaks of activation should become dominant among the rest for an accurate saccade to just one among alternative stimuli. This additional processing is selection of the target.

A network of structures in the visual pathway contributes to selecting targets for saccades. Neurons in primary visual cortex and extrastriate areas represent a variety of more or less elaborated features, surfaces and objects (chapters 25–28, 40, 41, 47, 55, 56), and these representations are influenced by the presence and nature of surrounding stimuli (chapter 30) and experience (chapter 70). Visual processing is not concluded in the parietal and temporal lobes, for extensive convergence of signals from numerous areas occurs in FEF (Markov et al., 2011; Schall et al., 1995) and SC (May, 2006). In fact, the latency of visual responses in FEF are comparable to those in middle temporal visual cortex (MT) and even precede the latencies of some neurons in V1 (Schmolesky et al., 1998). The density of neurons in the supragranular layers that project to area V4 resembles a feedforward connection (Barone et al., 2000) with terminals on dendritic spines, mainly in supragranular layers of V4 (Anderson, Kennedy, & Martin, 2011). Thus, FEF is positioned anatomically and temporally to influence neural processes in extrastriate visual areas. The influence conveyed by FEF to visual cortex is a central feature of network models of visual attention (e.g., Hamker & Zirnsak, 2006). However, recent evidence indicates that areas V4 and MT receive a different quality of influences from the frontal lobe (Ninomiya et al., 2012); thus, "top-down" modulation is not a unitary process.
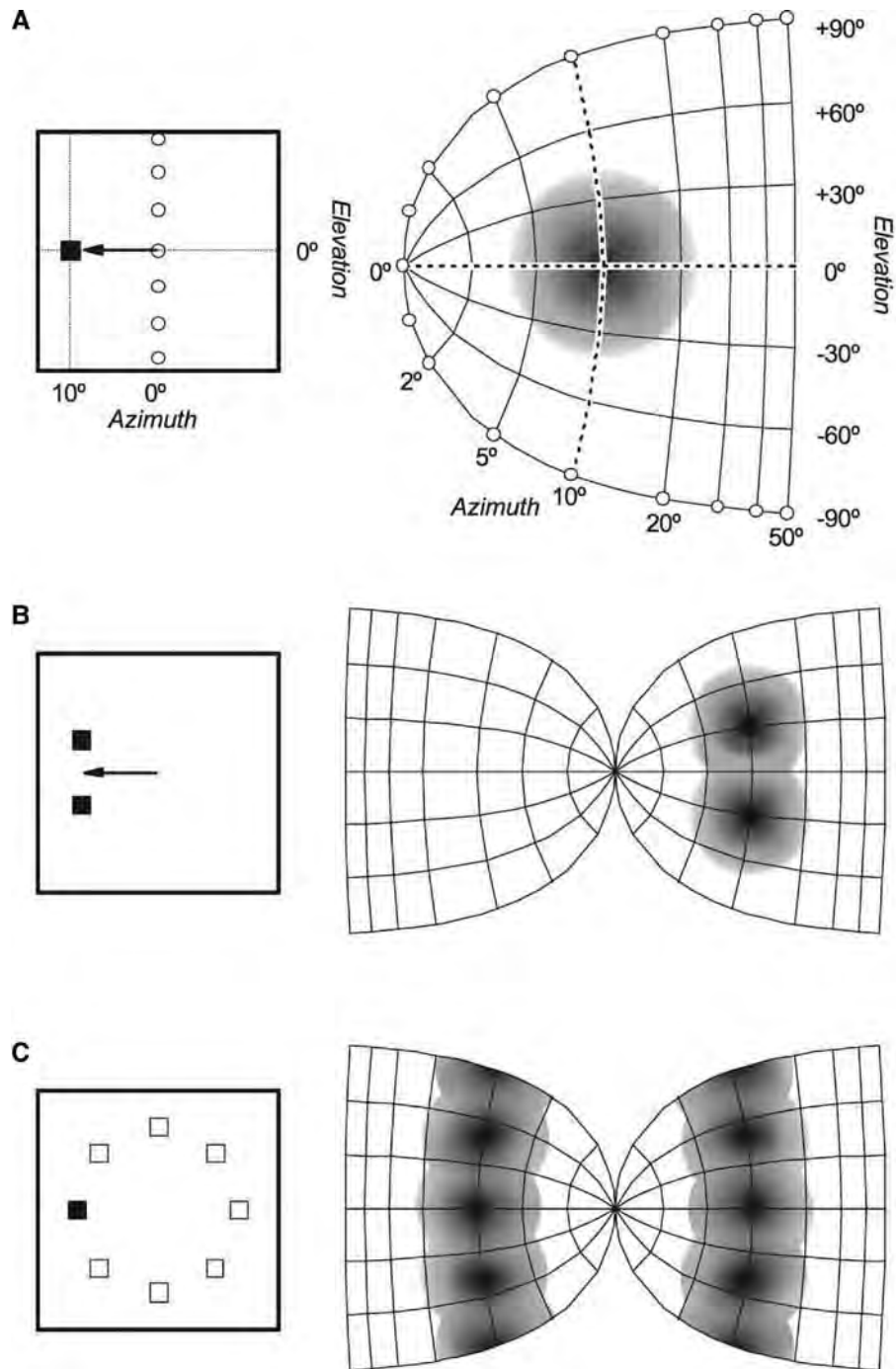
908   JEFFREY D. SCHALL

FIGURE 63.1   Pattern of presaccadic activation in the superior colliculus. (A) Left panel illustrates the visual field with a saccade (arrow) produced from the center to a target at 10° azimuth and 0° elevation. The vertical meridian is indicated by the row of circles. Right panel illustrates the map of the superior colliculus derived from a systematic survey of the direction and amplitude of saccades evoked by electrical stimulation of various parts of the superior colliculus. A visually guided saccade to a point 10° eccentric on the horizontal meridian is preceded by graded activation over an extended part of the superior colliculus map. The peak of activation (black) is centered at the appropriate point in the map, and surrounding neurons are progressively less active further from the center of activation (gray). The direction and amplitude of the saccade that is produced corresponds to that specified by the location of the center of gravity of the activation in the superior colliculus map. (B) Presentation of two nearby stimuli result in a broader zone of activation in the superior colliculus with two peaks. The center of gravity of the activation is a location in between the two stimuli. This results in a saccade directing gaze to neither stimulus. The map of the superior colliculus representing each hemifield is shown. (C) Presentation of eight stimuli produces activation in a large part of the superior colliculus map. The center of gravity of such balanced activation with multiple peaks amounts to a saccade with no amplitude. Thus, to produce a particular saccade, the activation in the superior colliculus map must evolve so that a single peak is present, corresponding to the desired saccade direction and amplitude.

SELECTION OF TARGETS FOR SACCADIC EYE MOVEMENTS   909

NEURAL CORRELATES OF TARGET SELECTION

Extensive research has demonstrated how neurons in cortical areas that represent stimulus features are modulated by target and surrounding nontarget features under various task demands (Bichot, Rossi, & Desimone, 2005; Buracas & Albright, 2009; David et al., 2008; Mirabella et al., 2007; Mruczek & Sheinberg, 2007; Ogawa & Komatsu, 2006; Saruwatari, Inoue, & Mikami, 2008). Another major input is top-down modulation based on goals and expectations enabled by neural circuits in the frontal lobe (Everling et al., 2006; Rossi et al., 2007; Zhou & Thompson, 2009).

We can define the functional salience map as the population of neurons that are not intrinsically feature selective but receive input from feature-selective neurons so that they signal the location of objects that are the target or are target-like in a manner that can be used to guide an action like an eye movement. According to this definition, compelling evidence obtained in multiple laboratories supports the conclusion that the neural representation of the salience map is distributed among multiple cortical areas and subcortical structures including FEF, parietal areas LIP and 7a, as well as the SC, basal ganglia, and associated thalamic nuclei. The heterogeneity of neural function within and diversity of connectivity between these areas makes clear that this salience representation is instantiated by an interconnected circuit built from some but not all of the neurons in these structures. Evidence that the selection process observed in these sensorimotor structures can be identified with a salience representation includes the following observations.

When a search array appears (either by flashing on during fixation or after a previous scanning saccade), activation increases at all locations in the map[2] corresponding to the potential saccade targets. This happens because these neurons are not naturally selective for visual features. Following the initial volley, activation becomes relatively lower at locations that would produce saccades to nontarget objects and is sustained or grows at locations corresponding to more conspicuous or important potential targets (see figure 63.2). This process has been observed independently by multiple laboratories in FEF (Cohen et al., 2009b; Lee & Keller, 2008; McPeek, 2006; Ogawa & Komatsu, 2006; Schall & Hanes, 1993), posterior parietal cortex (Balan et al., 2008; Buschman & Miller, 2007; Constantinidis & Steinmetz, 2005; Ipata et al., 2006; Ogawa & Komatsu, 2009; Thomas & Paré, 2007), SC (Kim & Basso, 2008; McPeek & Keller, 2002; Shen & Paré, 2007; White & Munoz, 2011a), substantia nigra pars reticulata (Basso & Wurtz, 2002), and ocular motor thalamic nuclei
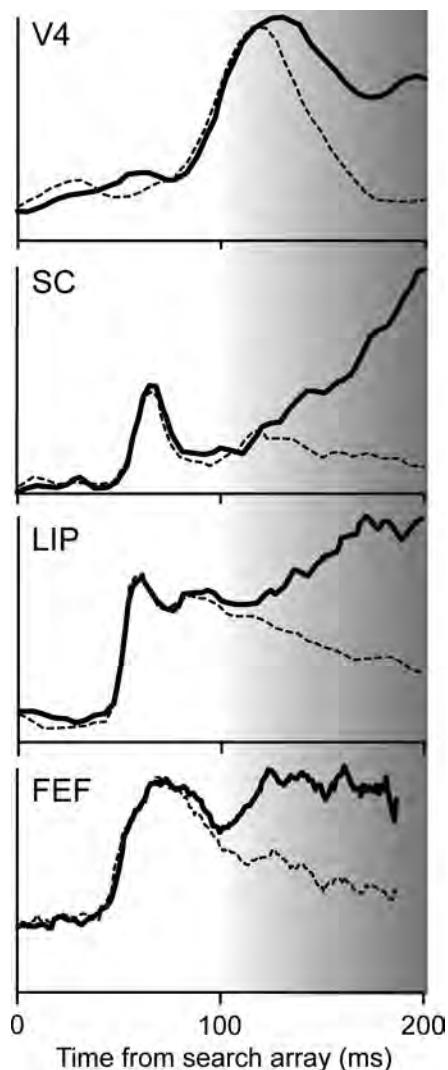

FIGURE 63.2   Illustration of visual and saccade target selection of representative single neurons in area V4 (adapted from Ogawa & Komatsu, 2004), superior colliculus (SC) (adapted from McPeek & Keller, 2002), lateral intraparietal area (LIP) (adapted from Thomas & Paré, 2007), and frontal eye field (FEF) (adapted from Thompson et al., 1996). 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 target was elsewhere (thin dashed line). Saccade target selection occurs in a distributed network of cortical and subcortical neurons.

(Schall & Thompson, 1994; Wyder, Massoglia, & Stanford, 2004). In these studies monkeys are responding to one among multiple alternatives for the purpose of earning reinforcement, usually with a single saccade. The target selection process has also been observed during natural scanning eye movements (Bichot, Rossi,

& Desimone, 2005; David et al., 2008; Phillips & Segraves, 2010; Zhou & Desimone, 2011). Microstimulation and inactivation have demonstrated causal roles in target selection of FEF (Monosov & Thompson, 2009; Wardak et al., 2006), SC (Lovejoy & Krauzlis, 2010; McPeek, 2008), and LIP (Balan & Gottlieb, 2009; Mirpour, Ong, & Bisley, 2010; Wardak, Olivier, Duhamel, 2004).

Manipulations that influence attention allocation in humans influence in parallel monkey performance and concomitant modulation of neural activity. For example, when search is less as compared to more efficient because target and distractor stimuli are more difficult to discriminate, then the selection process occupies more time and accounts for a greater proportion of the variability of reaction time (RT; Balan et al., 2008; Cohen et al., 2009b; Hayden & Gallant, 2005; Sato et al., 2001; Sato & Schall, 2003; Woodman et al., 2008). The well-known effects of target–distractor similarity on search performance that are expressed in response times and choices by macaque monkeys are paralleled in the magnitude and timing of the visual selection process measured in FEF neurons (Cohen et al., 2009b). When the target is more similar to distractors through either feature similarity or recent stimulus history, the level of neural activity in FEF representing the alternative stimuli is less distinct, leading to a higher likelihood of treating a distractor as if it were the target (Heitz et al., 2010; Thompson, Bichot, & Sato, 2005). This parallel suggests that the statement "less efficient allocation of attention" describes a state of the network in which the activity representing a target and distractors is less capable of being distinguished by either a neurophysiologist or a read-out circuit. Another influence believed to be mediated through the salience map is inhibition of return, the decreased likelihood of directing gaze to a location previously fixated. Neural correlates of this have been described in FEF (Bichot & Schall, 2002), LIP (Mirpour et al., 2009), and SC (Fecteau & Munoz, 2005).

The representation of salience is regarded to guide covert as well as overt orienting independent of effector. The neural selection of the target as a visual location to which to orient attention does not inevitably and immediately lead to reorienting of the eyes. It occurs if no overt response at all is made (Arcizet, Mirpour, & Bisley, 2011; Thompson, Bichot, & Schall, 1997) or if the saccade is directed away from a color singleton (Murthy et al., 2009; Sato & Schall, 2003). The selection process occurs as well if target location or property is signaled by a manual response (Ipata et al., 2009; Monosov & Thompson, 2009; Oristaglio et al., 2006; Thompson, Biscoe, & Sato, 2005).

POPULATION SIGNALS FOR TARGET SELECTION

Having identified key nodes in the network representing visual salience, further investigation of the mechanism has been accomplished. All of the results described above were based entirely on modulation of discharge rates of individual neurons. It is clear, though, that saccade target selection is accomplished by pools of neurons (Bichot et al., 2001; Kim & Basso, 2008, 2010) and probably entails more than just modulation of spike rate because cooperation and competition between pairs of neurons is modulated during target selection (Cohen et al., 2010). Indeed, correlation in discharge rates of FEF neurons over longer time scales has been reported even before stimulus presentation (Ogawa & Komatsu, 2010). Other researchers have measured local field potentials (LFP) in V4, LIP, and FEF during visual search and attention tasks and described increased coherence in the gamma band between spikes and LFP within and across areas such as V4, LIP, and FEF (Bichot, Rossi, & Desimone, 2005; Buschman & Miller, 2007; Gregoriou et al., 2009). Although argued to enhance the representation of attended objects, the functional utility of such signals is not undisputed (Ray & Maunsell, 2010).

An alternative analysis of LFPs is simply to measure the time course of differences in polarization when the target is in or out of the receptive field. This approach corresponds to the measurement of an event-related potential (ERP) on the scalp known as the N2pc that is a signature of the locus and time of attention allocation (Woodman & Luck, 1999). The N2pc has been found in macaque monkeys (Woodman et al., 2007). Source localization procedures indicate that the N2pc arises from parietal and occipitotemporal sources in humans (Boehler et al., 2011) and macaques (Young et al., 2010). In both efficient and inefficient search conditions the target is selected significantly earlier in neural spike rate modulation than in LFP polarization (Cohen et al., 2009a; Monosov, Trageser, & Thompson, 2008), and the delay varies with search efficiency. It appears that local processing within FEF mediated by spike rates results in delayed changes of synaptic potentials manifested in the LFP.

INTERACTIONS BETWEEN THE FRONTAL LOBE AND VISUAL CORTEX DURING TARGET SELECTION

I have described a target selection process that occurs more or less concurrently in multiple cortical areas and subcortical structures. Recent studies in macaque monkeys have investigated interactions between FEF

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and LIP (Buschman & Miller, 2007), V4 (Gregoriou et al., 2009, 2012; Zhou & Desimone, 2011), and inferior temporal (IT) cortex (Monosov, Sheinberg, & Thompson, 2010; Monosov & Thompson, 2009) as well as an ERP component recorded over visual cortex that indexes attention (Cohen et al., 2009a). While firm conclusions are premature because results were obtained with different tasks, neural signals, measurement procedures, and areas, some results seem consistent across laboratories. First, when search is inefficient, neural signals of attention allocation in FEF precede those in extrastriate visual areas. For example, a recent study demonstrated that spatial selection of a location in FEF precedes object recognition by IT neurons at that location (Monosov, Sheinberg, & Thompson, 2010) and the selection in FEF is necessary for detection and identification of the target (Monosov & Thompson, 2009). Similarly, the target selection observed in spike rate and LFP in FEF preceded the N2pc (Cohen et al., 2009a), and the delay between selection in FEF and visual cortex increased with the number of distractor stimuli, demonstrating that the delay is not due simply to conduction lags. These results expose a puzzling question—if different times of target selection are measured in different nodes of the network and scales of signal, then when would we say that attention has been allocated? Given the variation in selection time across neurons even within an area, can we say that the target is selected when the earliest, the latest, or some intermediate population of neurons resolve target location? Such a basic question highlights our profound uncertainty about how signals arise in and are conveyed between the areas representing features, objects, and salience.

This influence of FEF on visual cortex can influence the quality of attentive visual processing (Monosov & Thompson, 2009; Moore & Fallah, 2004). Weak electrical stimulation of FEF influences extrastriate visual cortex activity in a manner similar to what is observed when attention is allocated (Armstrong, Fitzgerald, & Moore, 2006; Ekstrom et al., 2009; Taylor, Nobre, & Rushworth, 2007; Walker, Techawachirakul, & Haggard, 2009).

FROM SALIENCE TO SACCADE

Explaining how sensory representations lead to accurate movements is a classic problem. One approach to this problem is based on the premise that noisy evidence guiding a response is accumulated over time until a threshold is achieved at which time the response is initiated (Ratcliff & McKoon, 2008; Usher & McClelland, 2001). A recent model inspired by this approach

provides an explanation for how signals from neurons that represent target salience can be transformed into a saccade command (Purcell et al., 2010, 2012) (see figure 63.3). The model uses the activity of visually responsive neurons in the FEF representing object salience as evidence for stimulus salience that is accumulated in a network of deterministic accumulators producing saccades to each possible target location to generate accurate and timely saccades during visual search. Response times are specified by the time at which the integrated signal reaches a threshold. The model included leak in the integration process and lateral inhibition between the ensemble of accumulators as well as a form of inhibition that gates the flow of perceptual evidence to the accumulators. Alternative model architectures were excluded because they did not fit the actual distributions of response times nor produce activation profiles corresponding to the form of actual movement neuron activity. At present, this is the only model of visual search that accounts for the range and form of response time distributions (Wolfe, Horowitz, & Palmer, 2010). This union of cognitive modeling and neurophysiology indicates how the visual–motor transformation can occur and provides a concrete mapping between neuron function and specific cognitive processes.

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 nontarget 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 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 (Pouget et al., 2011).

STIMULUS–RESPONSE MAPPING

The gated feedforward cascade model assumes that saccade production is guided entirely by the visual salience representation. Thus, errant saccades would be explained by failure to represent evidence correctly. While this has been observed in some testing conditions (Heitz et al., 2010; Thompson, Bichot, & Sato, 2005), several other lines of research demonstrate that the salience representation can be correct even if responses
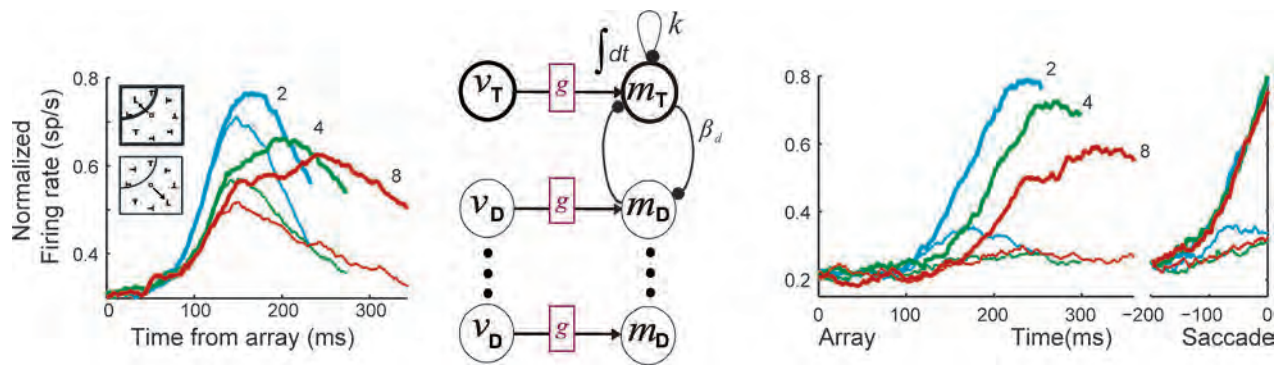
912   JEFFREY D. SCHALL

FIGURE 63.3   Object salience can be converted into saccade command through a gated accumulator network. Left: Data showing the evolving selective responses of visual salience neurons to the target "L" (thick) versus distractor "T" (thin) when presented in arrays of two (blue), four (green), or eight (red) objects. Middle: Gated accumulator model architecture in which the visual salience representation at the location of the actual target (vT) and distractors (vD) cascades into a network of units that produce saccades to the actual target location (mT) or distractor locations (mD) when their activation reaches a threshold. The activation accumulates through integration ($\int dt$) of the salience input limited by leak (k) and lateral inhibition (β). Right: Data showing accumulating activity of presaccadic movement neurons before saccades into (thick) and out of (thin) the movement field aligned on array presentation (left) and saccade initiation (right). The model replicated the dynamics of this accumulation process. (Adapted from Purcell et al., 2012.)

are incorrect. For example, in monkeys performing a saccade double-step task with visual search, visual neurons in the FEF locate the new location of the oddball in the search array correctly even when monkeys incorrectly shift gaze to the old location (Murthy et al., 2009). Similarly, when manual response errors occur, the selection process in FEF locates the singleton in the search array correctly (Trageser et al., 2008). However, if the brain located the new location of the oddball correctly, why was an error made? A plausible answer appeals to the hypothesis that the response production stage, although guided by the perceptual stage can operate independently of the perceptual stage. Further evidence for this is the fact that these errors can be corrected very rapidly, even before the brain can register that the gaze shift was an error (Murthy et al., 2007; see also Phillips & Segraves, 2010).

Saccade target selection has also been investigated under conditions that dissociate visual target location from saccade endpoint 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 & Schall, 2003). 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 responsive neurons were found 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 antisaccade. 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 dramatic modulation of discharge rate before the antisaccade was initiated (see figure 63.4A). After producing 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 (see figure 63.4B).

This experiment revealed a sequence of processes that can be distinguished in the modulation of different populations of neurons in FEF. The time course of these processes can be measured and compared across stimulus–response mapping rules (see figure 63.4C). To summarize, type I neurons selected the singleton earlier than did type II neurons, and the time of this selection 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
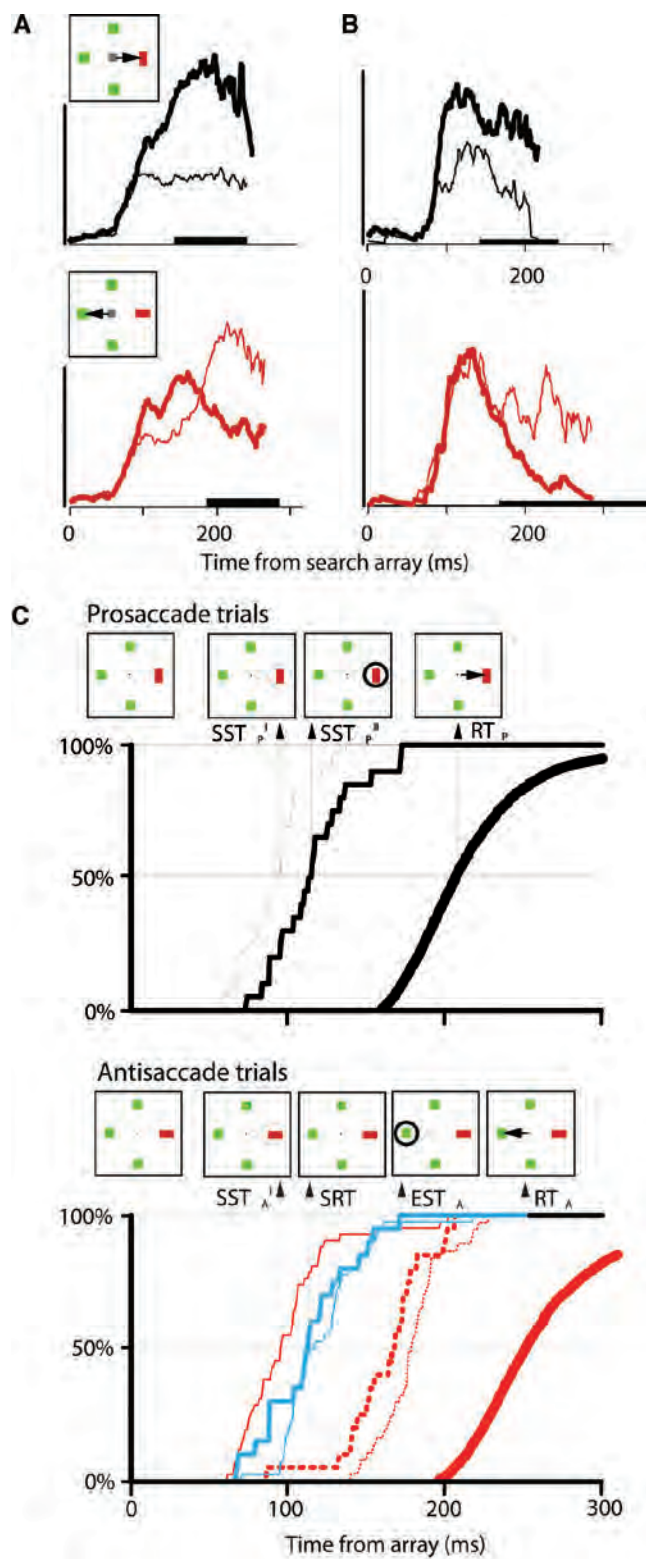
FIGURE 63.4 Elaboration of target selection process when mapping between location of visual target and endpoint of saccade is varied. (A) Activity of FEF neuron with activity indexing allocation of attention (type I). Average spike density function when the singleton fell in the neuron's receptive field (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 reaction time in prosaccade (RT_P) and in antisaccade (RT_A) trials. Scale bar represents 100 spikes/s. (B) Activity of FEF neuron with activity indexing 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, the singleton location is selected after a delayed labeled the singleton selection time (SST_P^I and SST_A^I) 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 (indicated by SST_P^{II}), 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, labeled the stimulus-response time (SRT). 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). In antisaccade trials, further modulation selects the endpoint of the saccade after a delay labeled endpoint selection time (EST_A) (indicated by the highlighted spotlight on the antisaccade endpoint). This is accomplished concomitantly by type I (thin, red, dashed) and type II (thicker red, dashed) neurons. The time taken to select the endpoint of the saccade predicts some of the delay and variability of RT. (Adapted from Sato and Schall, 2003.)

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 that 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 accounted for some but not all of the delay and

variability of RT. The results of this experiment demonstrate that the process of saccade target selection requires a number of representations and transformations beyond simply representing stimulus salience and producing a saccade.

TESTING THE PREMOTOR THEORY OF ATTENTION

If shifting visual spatial attention corresponds to preparing a saccade, then it should be impossible to dissociate saccade preparation from the focus of attention even if the endpoint of a saccade is directed opposite the attended stimulus. This was tested by probing the evolution of saccade preparation using electrical stimulation of the FEF (Juan, Shorter-Jacobi, & Schall, 2004). 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 (Sato & Schall, 2003). Saccade preparation was probed by measuring the direction of saccades evoked by intracortical microstimulation of the FEF 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. The interpretation of these results is framed by the findings described above, showing that on antisaccade trials most visually responsive neurons in FEF initially select the singleton while attention is allocated to distinguish its shape. Evidence consistent with these observations has been obtained in human participants using transcranial magnetic stimulation (Juan et al., 2008) and in a study probing explicitly the locus of attention (Smith & Schenk, 2007). Thus, the brain can covertly orient attention without preparing a saccade to the locus of attention. In other words, target selection and saccade preparation are distinct processes because they can be modified separately (Sternberg, 2011). This separate modifiability occurs because different populations of neurons carry out different functions as reviewed above.

Testing the premotor theory requires specifying the anatomical level at which the mechanism maps onto the brain. If shifting attention is accomplished by the same neurons that are preparing a saccade, and if saccade commands are issued by layer 5 pyramidal neurons in FEF, and if FEF influences attention by projections to areas V4 and TEO, then numerous layer 5 neurons must be double labeled by tracer injections in SC and V4/TEO. A recent study found, though, that whereas only pyramidal neurons in layer 5 projected to the SC, the large majority of neurons in FEF projecting to extrastriate visual cortex are located in layers 2 and 3, and no neurons were found projecting to both SC and visual cortex (Pouget et al., 2009). Thus, we can reject the premise that shifting attention is accomplished by the population of neurons that prepare saccades. This conclusion is based on a strict mapping between populations of specific types of neurons and the cognitive processes of attention allocation and saccade preparation. However, a theory formulated too generally to map onto specific neural types loses the relevance of mechanism and force of falsifiability. This result entails that FEF delivers different signals to the visual and ocular motor systems. What, then, is the nature of the influence of FEF on visual processing? If it is not a copy of the saccade command, what else could it be? Anatomical reconstruction of recording sites shows that neurons located in the supragranular layers of FEF are active during the process of attentional target selection (Thompson et al., 1996). Therefore, the kind of signal that extrastriate cortex receives from FEF is the target selection process described above that corresponds to the allocation of attention.

GENERAL 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 nontargets 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 nontarget 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 nontarget elements.

Coordinated with this visual processing is activation in a network including the FEF and SC that is responsible for producing the saccade. 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 ensure 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 nontarget 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.

Our understanding of how the visual system guides saccadic eye movements has improved considerably since the first version of this chapter appeared. While we continue to pursue remaining questions, we should retain our sense of marvel at the nimble and flexible manner of movements of these shiny globes of gristle that are called the windows to the soul.

NOTES

1. Some authors prefer the term "salience" to refer only to conspicuity in the image, and the additional influence of goals is enabled through a "priority" map. In other formulations the salience map combines bottom-up and top-down influences; we will use the latter formulation.
2. The quality of the visual field and saccade vector representation varies across these areas from very precise in SC (chapter 64) to clear but less precise in FEF (Bruce et al., 1985; Suzuki & Azuma 1983) to very imprecise in parietal areas (Ben Hamed et al., 2001).

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916   JEFFREY D. SCHALL

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918   JEFFREY D. SCHALL

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