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Visuomotor Functions in the Frontal Lobe

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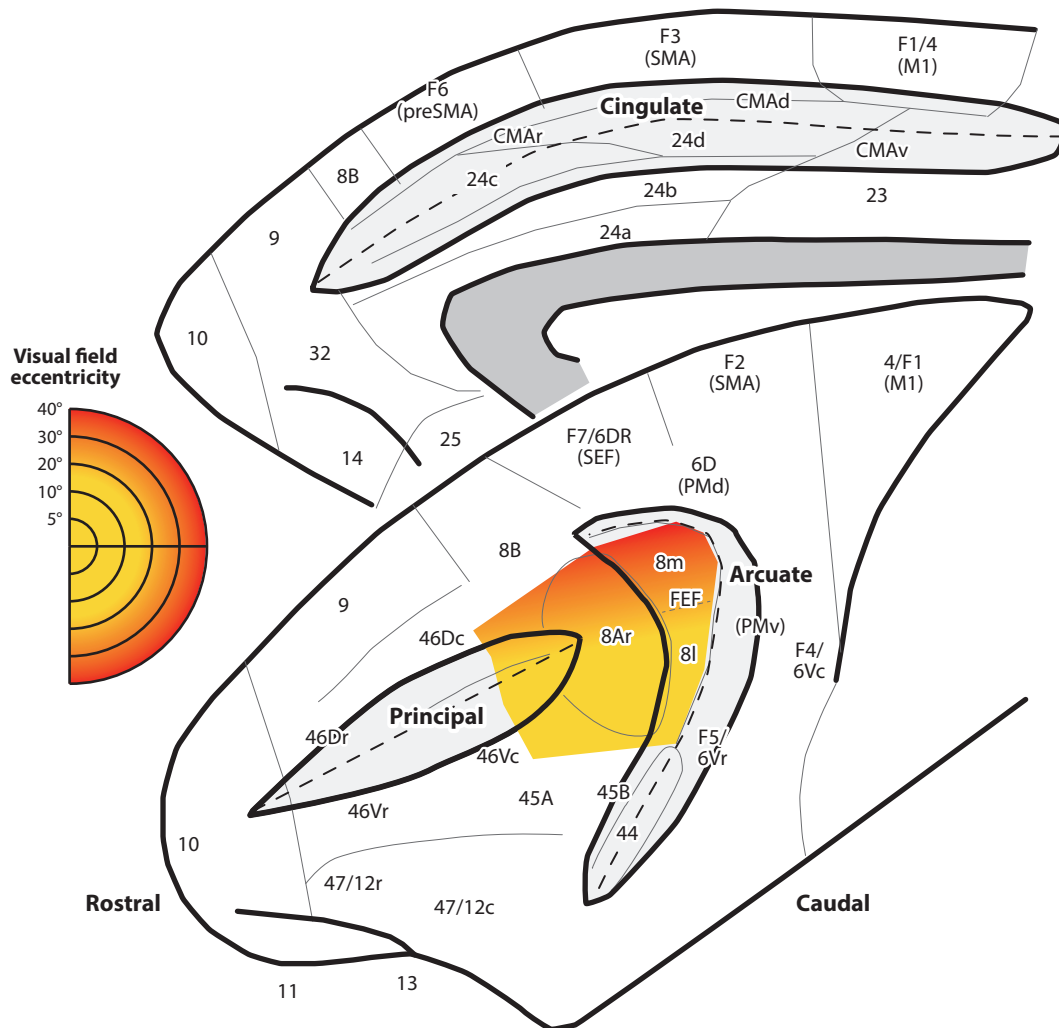
attention, categorization, decision, executive control, eye movement, memory, prefrontal cortex, premotor cortex, planning, visual search

Abstract

This review surveys how vision becomes action through the frontal lobe. Signals from extrastriate areas create maps in frontal areas. These maps are shaped by visual features and shaded by goals, values, and experience, and they guide contingent activation of motor circuits to execute coordinated gaze, head, and limb movements. Frontal circuits also support the visual perception of learned objects, events, and actions. Other frontal circuits monitor consequences and exert executive control to improve the effectiveness of visually guided behavior.

INTRODUCTION

Beginning with the work of Ferrier (1874) and accelerating with that of Bizzi, Fuster, Goldberg, Goldman-Rakic, Schiller, Schlag, Wurtz, and their colleagues (Bizzi & Schiller 1970, Fuster & Alexander 1971, Kojima & Goldman-Rakic 1982, Mohler et al. 1973, Schlag & Schlag-Rey 1970), the diverse contributions to vision made by the frontal cortex have become evident. Many neurons in the frontal cortex respond to visual stimuli, but the responses signal less about features than they do about context, value, and plan. Other neurons contribute to gaze shifts—both rapid and pursuit, conjugate and vergence—and to coordination of gaze with body movements. The frontal lobe mediates the flexible and adaptive mapping between vision, goals, actions, and consequences. This review updates an earlier survey (Schall 1997) to orient the reader to the past decade of this rapidly expanding literature, emphasizing neurophysiological studies of the macaque monkey because these studies provide the most mechanistic insights. The vast literature on human frontal lobe function is not incorporated here.



FRONTAL CORTEX ORGANIZATION

The frontal lobe contains multiple areas that have more or less distinct structures and functions. We begin with an orientation to the current understanding of frontal lobe layout before surveying the functions of the various areas.

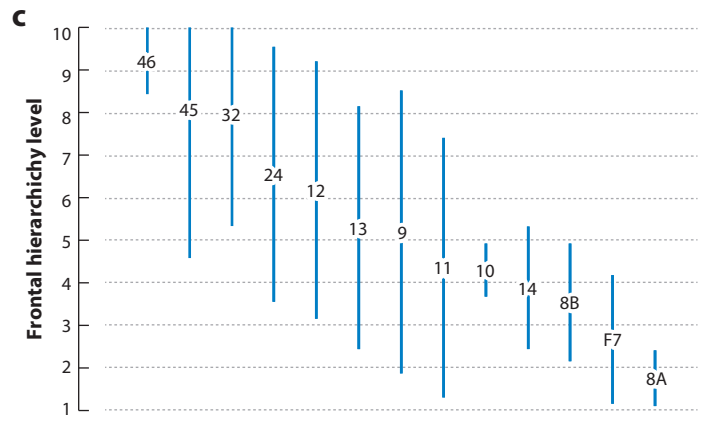
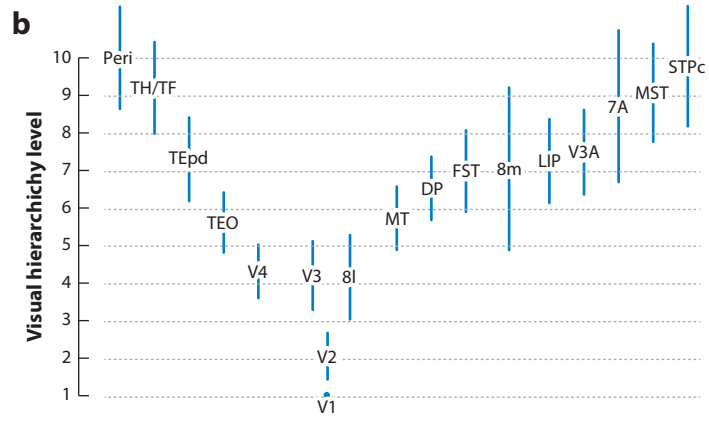
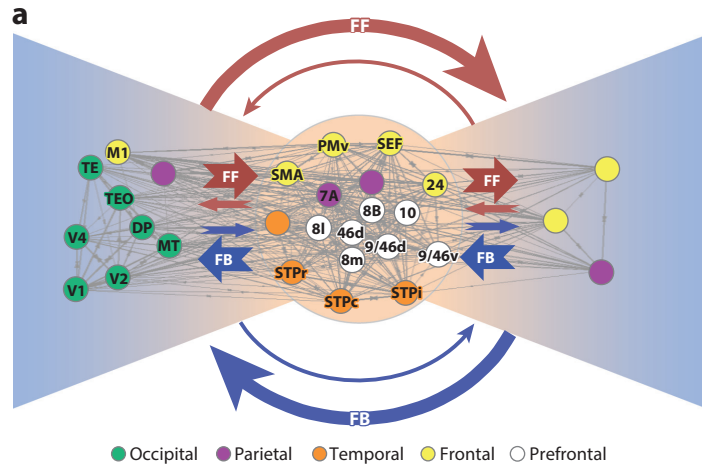
The frontal lobe can be partitioned into distinct areas on the basis of variation among several structural properties. The caudal frontal lobe is characterized by the presence of very large pyramidal cells in layer 5 (L5) and by the absence of granular layer 4 (L4) (but see Barbas & García-Cabezas 2015). The rostral areas are characterized by a dense L4 and by smaller pyramidal cells with a progressive increase in dendritic branches and spines (Elston 2003). Inhibitory interneuron density, distribution, and type also vary among frontal areas (Condé et al. 1994). The borders between many frontal lobe areas can be recognized with confidence, but the borders of others are less certain. **Figure 1** depicts a map of the macaque frontal lobe that incorporates most currently accepted subdivisions, many of which have counterparts in humans; this figure uses a mixture of nomenclatures (Dombrowski et al. 2001, Petrides et al. 2012, Sallet et al. 2013).

Recent studies have refined our understanding of many details of the connectivity among frontal areas and between frontal and extrastriate visual areas; many new insights have been earned from quantitative methods and graph theory algorithms (Barbas & Rempel-Clower 1997; Medalla & Barbas 2006; Modha & Singh 2010; Markov et al. 2013, 2014; Goulas et al. 2014; Saleem et al. 2014). Areas in the prefrontal cortex (PFC) form central nodes in the cortical network (**Figure 2a**). For example, area 8, which includes the frontal eye field (FEF), has one segment (lateral area 8l) situated at a low level of the visual area hierarchy and another segment (medial area 8m) at an intermediate level of it (**Figure 2b**), although area 8 is near the bottom of the hierarchy of prefrontal areas (**Figure 2c**). According to a variety of network measures, the highest level of the prefrontal hierarchy consists of lateral areas 46 and 45, medial areas 32 and 24, and orbital area 12. Thus, although the caudal pole is at the bottom of the visual area hierarchy, the rostral pole is not at the top of the frontal area hierarchy.

Cortical connections are specific because neurons, particularly those in layers 2 and 3 (L2/3), rarely project to more than one area. For example, different populations of neurons in the FEF

Figure 1

Areas of the macaque frontal lobe. This diagram emphasizes location and relation, not scale. The cingulate, principal, and arcuate sulci are illustrated with exposed fundus (*dashed line*) and banks (*gray*). Area boundaries are indicated. Immediately rostral to the central sulcus is Brodmann's area 4 or F1, which is known functionally as the primary motor cortex (M1). Rostral to M1 is Brodmann's area 6, which is subdivided into several areas. The supplementary motor area (SMA), which occupies dorsal area F2 and mesial area F3, is located on the medial wall and dorsal convexity. Rostral to the SMA on the medial wall is the preSMA (F6). Rostral to SMA on the dorsal convexity is the supplementary eye field (SEF), which occupies medial area F7. Area 24 is ventral to the SMA and preSMA and is subdivided into four architectonic subregions. Three zones within area 24 and caudally adjoining area 23 are referred to as cingulate motor areas (CMAs). The rostral boundary of the preSMA and the SEF meets granular prefrontal area 8B. Area 9, which forms part of the caudal boundary of area 10, is rostral to area 8B. The dorsal premotor area (PMd, architecturally labeled 6D or lateral F2 and F7) is lateral to the SMA and SEF and caudal to the arcuate sulcus. The ventral premotor area (PMv) can be further subdivided into rostral (F5/6Vr) and caudal (F4/6Vc) areas. In the fundus of the arcuate sulcus, agranular area 6 transitions to granular area 8. The rostral bank of the arcuate sulcus, caudal to the principal sulcus, is occupied by the frontal eye field (FEF), which consists of a medial area, 8m, and a lateral area, 8l. The FEF embodies a map of saccade amplitude: The shortest saccades are represented laterally (in 8l) and the longest saccades, medially (8m). The convexity between the arcuate and principal sulci is occupied by area 8Ar, so named because it is distinct from the more rostral area 46, which is itself subdivided into the caudal areas 46Dc and 46Vc and rostral areas 46Dr and 46Vr. A map of visual field eccentricity (indicated in color) occupies the rostral bank of the arcuate sulcus, adjacent prearcuate convexity, and the caudal portion of the principal sulcus. Area 45B, located on the lip and rostral bank of the arcuate sulcus, and area 44 in the fundus are lateral to area 8l. Area 45A is lateral to area 8Ar. Area 47/12, which extends onto the ventral surface of the frontal lobe, is ventral to area 46. Area 12 borders areas 11 and 13, which occupy the orbitofrontal cortex. The rostral pole is area 10.



project to visual area V4 and the medial temporal area (MT), and those projecting to V4 receive input from area 46v, whereas those projecting to MT receive input from both area 46v and the supplementary eye field (SEF) (Ninomiya et al. 2012). Findings such as these contradict the hoary dictum that “everything is connected to everything” and should highlight the enormous gap between the low-resolution functional descriptions of various brain areas and the specificity and diversity of high-resolution anatomical descriptions.

Connectivity is one constraint; time is another. The relative latencies of responses across visually responsive areas do not correspond to sequential activation through an anatomical hierarchy (**Figure 3**) (Schmolesky et al. 1998, Pouget et al. 2005). For example, the visual response latencies in the FEF overlap those in V1, V2, V3, V4, MT, and the medial superior temporal area (MST). Hierarchical connectivity and response timing have been reconciled at least partially by emphasizing shortest routes (Petroni et al. 2001) and by incorporating subcortical connections that can convey rapid visual responses (Capalbo et al. 2008).

FRONTAL EYE FIELD

The frontal eye field (FEF) is located in the rostral bank of the arcuate sulcus in monkeys, and this area is found in a corresponding location in the middle frontal gyrus at the intersection of the superior precentral sulcus and the superior frontal sulcus in humans (Koyama et al. 2004, Amiez & Petrides 2009). In monkeys, it is identified in area 8, but in humans, it is identified in area 6. This difference is more a matter of criteria, however: The cytoarchitecture of the human FEF

Figure 2

Connectivity of frontal areas. (a) Hierarchical feedforward (FF) (red arrows) and feedback (FB) (blue arrows) cortical connectivity. Premotor and prefrontal areas form a highly connected core that receives predominantly feedforward inputs from extrastriate visual areas; these inputs are reciprocated with predominantly feedback inputs (left wing). The core areas deliver predominantly feedforward inputs to other cortical areas that in turn provide feedback (right wing). Panel adapted from Markov et al. (2013). Cortical high-density counterstream architectures. *Science* 342:1238406. Reprinted with permission from AAAS. (b) Hierarchy of visual areas. The lateral frontal eye field (FEF) (8l), which produces shorter saccades, is at the same level as V3 and V4, whereas the medial FEF (8m), which produces longer saccades, is at the same level as TE, LIP, V3A, and FST. Anatomically, the FEF is feedforward to several occipital, parietal, and temporal areas. Panel adapted with permission from Markov et al. (2014). (c) Hierarchy of prefrontal areas. In this hierarchy, the top of the anatomical hierarchy comprises lateral frontal areas 46 and 45 and medial area 32. Area 8A, which includes the FEF, is the lowest lateral frontal area. Panel adapted with permission from Modha & Singh (2010) and Goulas et al. (2014). Division into 10 levels is arbitrary. Error bars represent the range of possible solutions; those in panel b are 95% confidence intervals, and those in panel c are the standard deviations of the range of alternative rankings assessed by the author. Areas are identified by an inconsistent system of numbers, defined abbreviations, and names based on location or function. The numbers follow and elaborate on Brodmann's original scheme as indicated in **Figure 1**. For example, V1, V2, V3, and V4 designate the primary, secondary, third, and fourth visual areas, respectively; V3A is distinguished from neighboring area V3. M1 indicates the primary motor cortex (also known as F1). Some abbreviations are defined based on location; these include the following: DP, dorsal parietal area; FST, fundus of superior temporal sulcus; LIP, lateral intraparietal area; MT, middle temporal area; MST, medial superior temporal area; Peri, perirhinal cortex; STPc, caudal superior temporal polysensory area; STPl, lateral superior temporal polysensory area; STPr, rostral superior temporal polysensory area; TE, temporal area; TEpd, posterior dorsal TE; TEO, temporal-occipital area; and TH/TF located on the ventral temporal lobe. Abbreviations derived from Brodmann's numbered areas include 7A (distinguished from a more rostral area 7B), 8A (distinguished from a more rostral and dorsal area, 8B), 8l (indicating lateral area 8), 8m (indicating medial area 8). Remaining areas are given functional names: PMv, ventral premotor area; SEF, supplementary eye field (within area F7); SMA, supplementary motor area.

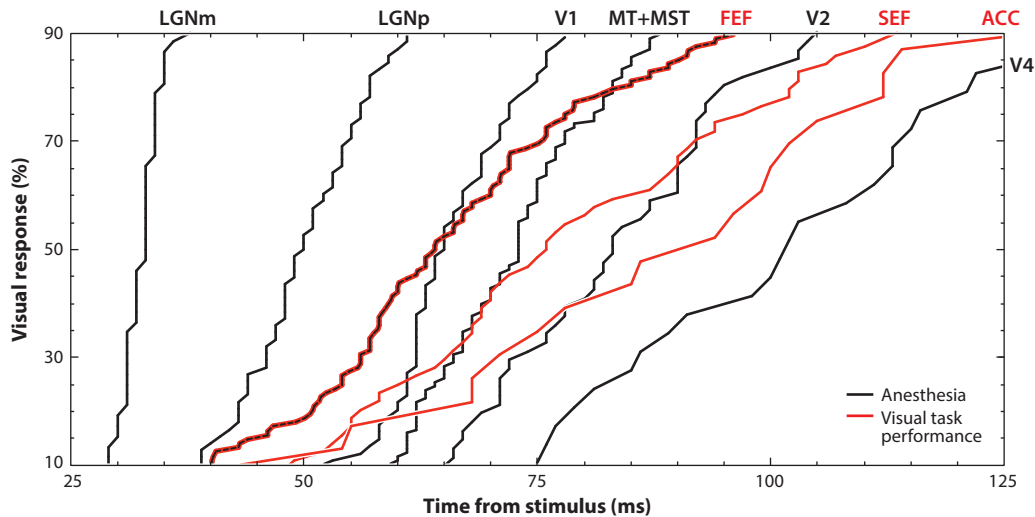


Figure 3

Latencies of response to a visual stimulus in the receptive field for neurons sampled from the indicated stations of the visual pathway measured under anesthesia (*black*) or during visual task performance (*red*); data from the frontal eye field (FEF) have been combined across both states. In the afferent pathway, the earliest responses are measured in the magnocellular and parvocellular layers of the lateral geniculate nucleus (LGNm and LGNp, respectively), followed by responses in primary visual cortex (V1), the medial temporal and medial superior temporal areas (MT+MST), and visual areas V2 and V4. In the frontal lobe, the earliest visual responses occur in the FEF, followed by responses in the supplementary eye field (SEF) and the anterior cingulate cortex (ACC). Figure adapted and replotted with permission from Thompson et al. (1996), Schmolesky et al. (1998), and Pouget et al. (2005).

corresponds to that of macaques, distinguished in both organisms by a less distinct granular L4 compared with more rostral areas and by clusters of large pyramidal cells in L5 (Rosano et al. 2003).

Generation of Eye Movements

Findings from studies using neural recordings, electrical stimulation, and pharmacological or thermal inactivation demonstrate the contribution of the FEF to saccadic eye movements in macaques (Bruce et al. 1985, Hanes & Schall 1996, Peel et al. 2014). In the macaque FEF, shorter saccades are represented laterally in the arcuate sulcus, and longer saccades are represented medially. Curiously, a different map has been reported in humans (Kastner et al. 2007). This map of saccade amplitude in macaques corresponds to the variation in connectivity observed between areas 8l and 8m (Schall et al. 1995, Babapoor-Farrokhran et al. 2013). Saccade amplitude at the boundary between areas 8l and 8m is $\sim 15^\circ$, which neatly partitions the FEF segment responsible for scrutinizing vision (8l) from that responsible for exploratory vision (8m). Saccades with amplitudes of less than $\sim 15^\circ$ are used during inspection and manual manipulation, and these saccades tend to be made without head movements. In contrast, longer saccades redirect gaze accompanied by head movements to which the FEF contributes (Chen 2006, Knight 2012, Monteon et al. 2013). FEF activity can be modulated by reaching movements and forelimb position in the natural workspace (Lawrence & Snyder 2009, Thura et al. 2011). A region contributing to coordinated ear and eye movements is dorsomedial to the FEF in areas 8B and 9 (Lanzilotto et al. 2013). Finally, a caudal region within the FEF contributes to pursuit eye movements (Fukushima et al. 2006, Ono &

Mustari 2009), and a rostral portion of the FEF contributes to vergence eye movements (Gamlin & Yoon 2000).

The FEF contributes to eye movements as a node in a circuit involving the basal ganglia, the thalamus, the superior colliculus (SC), and the brainstem. L5 neurons in the FEF project to pontine and mesencephalic brainstem nuclei (Segraves & Goldberg 1987, Segraves 1992, Sommer & Wurtz 2000). These projections terminate on presaccadic neurons in the SC (Helminski & Segraves 2003), and presaccadic movement activity returns to the FEF via the thalamus (Sommer & Wurtz 2004).

Intriguingly, although the FEF is capable of initiating saccades following SC ablation (Schiller et al. 1980), the FEF cannot initiate saccades during SC inactivation in the intact brain (Hanes & Wurtz 2001). Still, the modulation of FEF movement neurons parallels that of SC movement neurons (and vice versa) when a monkey is tested in common tasks. For example, the activity of movement neurons in both the FEF and the SC is lower before antisaccades than before prosaccades (Everling & Munoz 2000). The FEF also contributes to gaze control by delaying or interrupting the initiation of eye movements (Hasegawa et al. 2004, Izawa et al. 2011); this delay is mediated by gaze-holding fixation neurons (Hanes et al. 1998, Izawa et al. 2009). The role of the FEF and the SC in controlling saccade initiation has been investigated thoroughly in monkeys performing a task that required them to interrupt saccade preparation on a random subset of trials in response to a new stimulus. A mathematical race model that accounts for performance of this saccade-countermanding task provides unique theoretical leverage for distinguishing between neurons that can contribute to the control of saccade production and those that cannot (Hanes & Schall 1996, Hanes et al. 1998, Paré & Hanes 2003, Murthy et al. 2009, Costello et al. 2013).

Visual Processing, Remapping, and Target Selection

The FEF is also a visual area. As noted above, visual responses in the FEF can have very short latencies. These short-latency responses are very sensitive, being immune to masking (Thompson & Schall 2000; cf. Libedinsky & Livingstone 2011) but often suppressed by repetitive flashes (Mayo & Sommer 2008). The earliest FEF visual responses seem to be of cortical origin because the thalamic input from the mediodorsal nucleus of the thalamus is too slow (Sommer & Wurtz 2004).

Neurons in the FEF typically do not exhibit much feature selectivity, although some show tuning for motion direction and an overrepresentation of radial direction preferences, perhaps to guide gaze through optic flow (Xiao et al. 2006). Visual motion signals in the FEF somehow modulate presaccadic activity according to target velocity to guide saccades to moving objects (Cassanello et al. 2008). Under particularly restrictive training conditions, FEF neurons can exhibit selectivity for features and objects (Bichot et al. 1996, Peng et al. 2008).

FEF neurons have large but bounded receptive fields that are concentrated in the contralateral hemifield and that represent the visual field, with the central visual field in the later FEF (8l) and the peripheral visual field in the medial FEF (8m), paralleling the representation of saccade amplitude (Suzuki & Azuma 1983). Some FEF neurons have ipsilateral receptive fields constructed from projections from the contralateral SC (Crapse & Sommer 2009). Similar to other visual areas, the receptive fields of FEF neurons have suppressive surrounds (Schall et al. 2004, Cavanaugh et al. 2012), and many FEF neurons have extraretinal influences such as reward magnitude (Ding & Hikosaka 2006) and predicted stimulus motion (Xiao et al. 2007).

The receptive fields of some FEF neurons appear to shift to the location that will be in the receptive field after a saccade (Sommer & Wurtz 2008, Joiner et al. 2013, Zirnsak et al. 2014), providing a signal for visual stability (Crapse & Sommer 2012). This modulation is also seen in

parietal areas and in the SC, and it is believed to underlie the stable perception of space that could be disrupted by saccadic eye movements. One source of this modulation in the FEF is a corollary discharge signal from the SC, which is conveyed through the mediodorsal nucleus of the thalamus (Sommer & Wurtz 2004). Studies of the modulation described above involve monkeys shifting gaze to a fixed location in an impoverished visual environment. The modulation is weaker when the image has more stimuli and structure (Joiner et al. 2011); these conditions afford greater visual stability based on the image itself and memory (Deubel et al. 2010, Tatler & Land 2011).

Several studies have described how FEF neurons contribute to visual discrimination in categorization tasks (Ferrera et al. 2009, Ding & Gold 2012, Mante et al. 2013). Many others have described how FEF neurons accomplish visual search for a target among multiple distractors (Thompson et al. 2005, Buschman & Miller 2007, Cohen et al. 2009, Monosov & Thompson 2009, Zhou & Desimone 2011, Gregoriou et al. 2012). When presented with an array of visual objects, one of which is a defined target, most visual neurons in the FEF initially respond indiscriminately. Before a saccade to the target, however, these neurons represent the location of the target with comparatively greater activity relative to that representing the locations of nontarget objects. This target selection process occurs during unconstrained scanning behavior, but it has different dynamics, which are related to sequential saccade production (Phillips & Segraves 2010, Zhou & Desimone 2011). Target selection in the FEF involves spike timing cooperation and competition (Cohen et al. 2010), as well as modulation of spike–field coherence (Buschman & Miller 2007, Gregoriou et al. 2012, Heitz & Schall 2013). Selection activity in the FEF is strongly modulated by speed–accuracy cues (Heitz & Schall 2012). Inactivation of the FEF impairs target selection in saccade choice tasks (Keller et al. 2008) and in both efficient and inefficient visual search tasks that do not require gaze shifts (Wardak et al. 2006).

The target selection process can influence saccade trajectory (McPeck 2006), but the selection observed in visual neurons has been experimentally dissociated from saccade production (Sato & Schall 2003, Thompson et al. 2005, Murthy et al. 2009, Ramakrishnan et al. 2012, Costello et al. 2013, Lee et al. 2012). Many researchers have described FEF contributions to guidance of covert attention (Juan et al. 2004, Zhou & Thompson 2009, Khayat et al. 2009, Squire et al. 2013), inspiring the claim that the FEF embodies a salience map (Thompson & Bichot 2005).

The timing of this target selection process varies according to stimulus properties and task demands. Target selection is delayed when search is less efficient because target and nontarget objects have similar appearances or when more nontarget objects are presented (Cohen et al. 2009b, Lee & Keller 2008). The target selection process is also more elaborate and delayed when stimulus–response mapping is more complex (Sato & Schall 2003).

Several laboratories have timed the target selection process across cortical areas and measurement levels in various tasks (**Figure 4**). Most of these studies have focused on the FEF and areas in the back of the brain, and the task design and measurement method used vary widely from study to study. Every study has found that when the target is more difficult to locate, neurons in the FEF and in the dorsolateral PFC (dlPFC) signal its location either before or as early as neurons in occipital, parietal, and temporal areas do (Buschman & Miller 2007, Cohen et al. 2009a, Monosov et al. 2010, Zhou & Desimone 2011, Gregoriou et al. 2012, Ibos et al. 2013, Pooresmaeili et al. 2014). This conclusion is based on chronological comparison of not only single-unit modulation times but also intracortical local field potentials and the N2pc event-related potential (ERP), which is identified with the allocation of visual attention (Woodman et al. 2007). Findings have differed, however, when the target is located easily in a color pop-out search—one study reports that the parietal cortex locates the target before the frontal cortex does (Buschman & Miller 2007), but two studies report otherwise (Katsuki & Constantinidis 2012, Purcell et al. 2013). Possible reasons

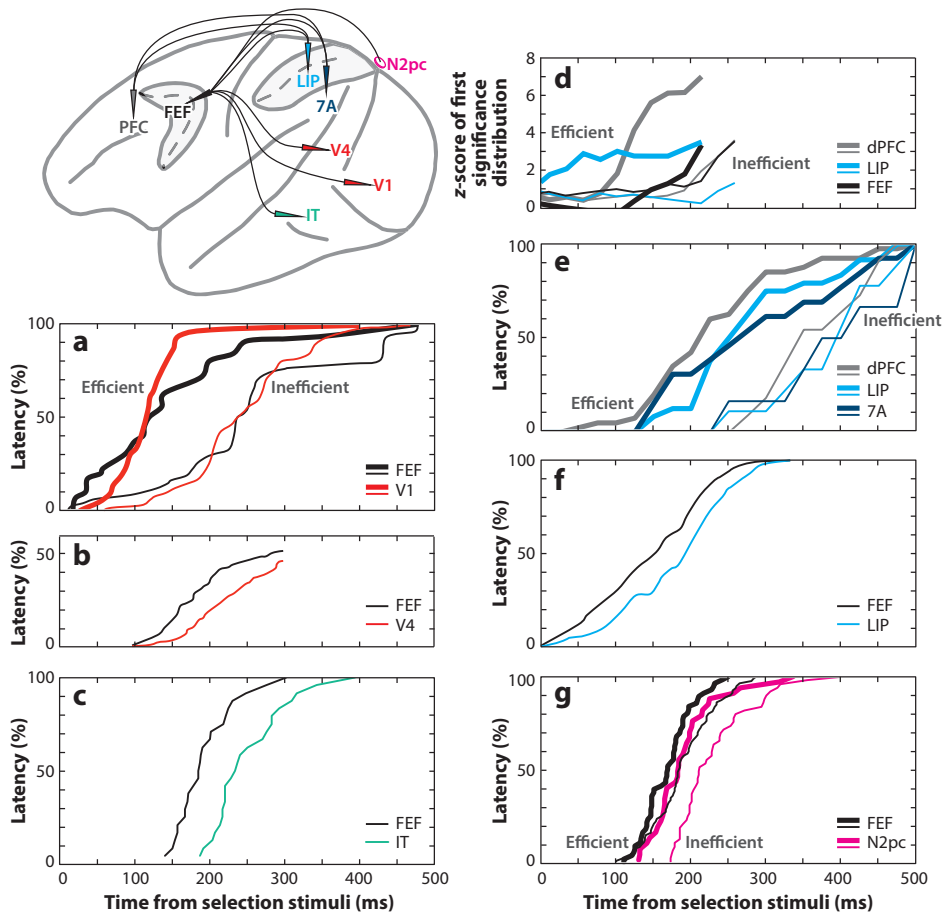


Figure 4

Target selection times across the visual pathway. Pairs of frontal and caudal areas sampled across laboratories are indicated; the disk represents a cranial event-related potential (ERP) recording. Only selection times preceding the behavioral response time are plotted. (a) Latency of target selection by frontal eye field (FEF) (black) and primary visual cortex (V1) (red) neurons in a line-tracing task when the target was more (thick) or less (thin) efficiently located. Note the delay in both areas in the less-efficient condition but the coincidence of latencies across areas in both conditions. Panel adapted with permission from Pooresmaeila et al. (2014). (b) Latency of target selection by FEF (black) and V4 (red) neurons during an inefficient visual search task. Note the delay of V4 relative to FEF neurons. Panel adapted with permission from Zhou & Desimone (2011). (c) Latency of target selection by FEF (black) and inferior temporal (IT) (green) neurons during an inefficient visual search task. Note the delay of IT relative to FEF neurons. Panel adapted with permission from Monosov et al. (2010). (d) Latency of target selection by FEF (black), lateral intraparietal (LIP) (light blue), and dorsal prefrontal cortex (dPFC) (gray) neurons during efficient (thick) and inefficient (thin) visual search. Note the delay of LIP neurons relative to FEF and dPFC neurons during inefficient search and the precedence of LIP neurons during efficient search. Panel adapted with permission from Buschman & Miller (2007). (e) Latency of target selection by dPFC (gray), LIP (light blue), and 7A (dark blue) neurons during efficient (thick) and inefficient (thin) visual search. Note the delay of LIP and 7A neurons relative to dPFC neurons during both efficient and inefficient search. Panel adapted with permission from Katsuki & Constantinidis (2012). (f) Latency of target selection by FEF (black) and LIP (light blue) neurons during a rapid serial visual presentation task. Note the delay of LIP relative to FEF neurons. Panel adapted with permission from Ibos et al. (2013). (g) Latency of target selection measured in FEF neurons (black) and the N2pc ERP (magenta) indexing attention allocation during efficient (thick) and inefficient (thin) visual search. Panel adapted with permission from Cohen et al. (2009) and Purcell et al. (2013).

for this difference in results have been considered, including optimization of stimuli for specific receptive field locations and measurement methods (Schall et al. 2007, Miller & Buschman 2007).

Because it responds to stimuli and selects targets so early, the FEF can influence processes in occipital, parietal, and temporal areas. The influence of the FEF on processes occurring in the back of the brain has been demonstrated vividly: Stimulation of the FEF can influence visual processing (e.g., Ekstrom et al. 2009) and the allocation of visual spatial attention through modulation of neural activity in extrastriate visual areas (reviewed by Squire et al. 2013). Other studies have shown how the FEF influences object identification performance and representations in the inferotemporal cortex (IT) during search (Monosov & Thompson 2009; Monosov et al. 2010, 2011).

The influence of the FEF on V4 appears to be mediated primarily by L2/3 (Noudoost & Moore 2011), that is, by visual neurons, not visuomotor or movement neurons (Gregoriou et al. 2012). The supragranular neurons projecting to V4 do not send inputs to the brainstem (Pouget et al. 2009). These findings sharply limit the scope of the premotor theory of attention. Recall that V4 and MT (and likely LIP and MST, among others) are innervated by different neurons in L2/3 of the FEF, and these neurons themselves have qualitatively different afferents (Ninomiya et al. 2012). Thus, the so-called top-down signals from the FEF to each extrastriate area likely convey functionally different influences.

Visual behavior is guided by experience. The target selection process in the FEF is influenced in parallel with search performance by immediate (Bichot & Schall 2002), intermediate (Bichot & Schall 1999), and long-term (Bichot et al. 1996) stimulus and response history, mediated in part by dopaminergic mechanisms (Soltani et al. 2013). A core function of the PFC, including the FEF, is maintaining task information in working memory. Many neurons in the FEF exhibit sustained activity during an instructed delay period (Lawrence et al. 2005, Clark et al. 2012), contributing to an ERP recorded over the parietal and occipital lobes that indexes spatial working memory for saccades (Reinhart et al. 2012).

The various representations, modulations, and transformations within and between nodes of the visuomotor network have been incorporated into circuit models of the FEF and associated structures (Mitchell & Zipser 2003, Brown et al. 2004, Hamker 2005, Heinzle et al. 2007) (**Figure 5**). Although these models are certainly not correct in detail, they fertilize the formulation of hypotheses to guide further research. Other models have explained FEF functions at a more abstract level (**Figure 6**). For example, the mathematical race model that accounts for performance of tasks requiring interruption or reprogramming of partially prepared saccades (Logan & Cowan 1984) has been instantiated in highly constrained neural network architectures of an interactive race between gaze-shifting movement neurons and gaze-holding fixation neurons (Boucher et al. 2007, Lo et al. 2009, Ramakrishnan et al. 2012, Salinas & Stanford 2013, Logan et al. 2015). The core features of this model probably also explain interruption and reprogramming of limb movements. Finally, a gated accumulator model of visual search describes how the activity of neurons representing object salience for target selection can be used as the evidence driving the accumulation embodied by the presaccadic movement neurons (**Figure 7**) (Purcell et al. 2010, 2012a; cf. Ding & Gold 2012). These models provide explicit, focused, and compelling translations between computational and neural levels of description.

MEDIAL FRONTAL CORTEX

This section describes the supplementary eye field (SEF) and anterior cingulate cortex (ACC). Compared with the FEF, the SEF and ACC receive many fewer visual afferents, but visual

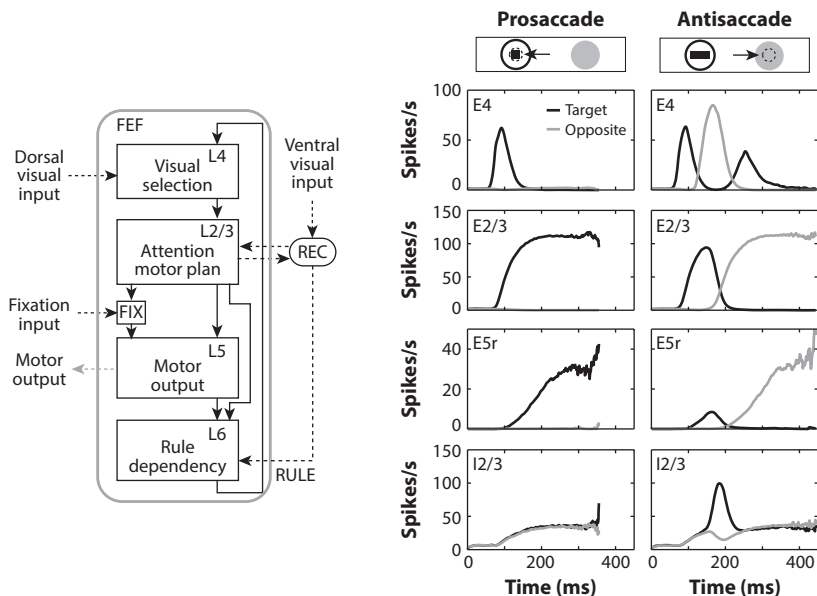


Figure 5

Microcircuit model of the frontal eye field (FEF) based on the circuitry of the primary visual cortex. The left panel diagrams the architecture of the circuit, and specific functions are mapped onto distinct layers operating in sequence. L4 receives nonselective input from areas in the dorsal stream and forms a transient visual salience map. L2/3 transforms the L4 representation into sustained attention allocation at the target to identify its feature(s). If a feature calls for an attention shift, the rule is registered by L6 and implemented through another cycle of L4 to L2/3 activation. Inhibitory neurons in L2/3 do not show selectivity for the position of the target in prosaccade trials, but they do signal the shift of the attention in antisaccade trials. L2/3 neurons drive L5 movement neurons, which provide the motor output. L6 provides a top-down salience signal based on arbitrary stimulus–response rules to activate L4 in the absence of visual input in antisaccade trials. L6 saccade neurons project to inhibitory neurons in L4 with two components: a fast global reset of L4 neurons, which resets the network after each saccade, and a slow selective drive, which implements inhibition of return. L5 consists of both buildup and burst neurons. L5 burst neurons provide excitatory input to inhibitory neurons in L2/3 that represent all locations except the fovea; these neurons also excite the fixation neurons in L2/3 to reset attention back to the fovea after each saccade. This model predicts a definite sequence of activation in different tasks. For visually guided prosaccades, L4 is activated earliest; L6 is activated latest by the L5 saccade burst. In addition, L4 activity is inhibited before saccade initiation, whereas L2/3 activity persists until the saccade. For antisaccades, an early response in L4 for the visual target is followed by a larger response in L4 at the location of the saccade end point. The latter response is driven by a large response in L6 at the visual cue location and by the lack of activation at the saccade end point. L6 activity is greater before antisaccades than before prosaccades. The right panel illustrates the activation of units in different layers representing the target location (*black*) and the opposite location (*gray*) for prosaccade (*left*) and antisaccade (*right*) simulations. In prosaccade trials, excitatory neurons in L4 and L2/3 represent the target location, and excitatory neurons in L5 produce the prosaccade. Meanwhile, inhibitory neurons in L2/3 signal the outcome of the recognition module that was equivalent for both locations. In antisaccade trials, excitatory neurons in L4 and L2/3 first represent the target location, then the opposite location. Inhibitory neurons in L2/3 differentially suppress the location of the target, allowing the enhanced representation of the antisaccade location. Excitatory neurons in L5 are activated briefly for the target end point, but they eventually produce the antisaccade. Figure adapted with permission from Heinzle et al. (2007).

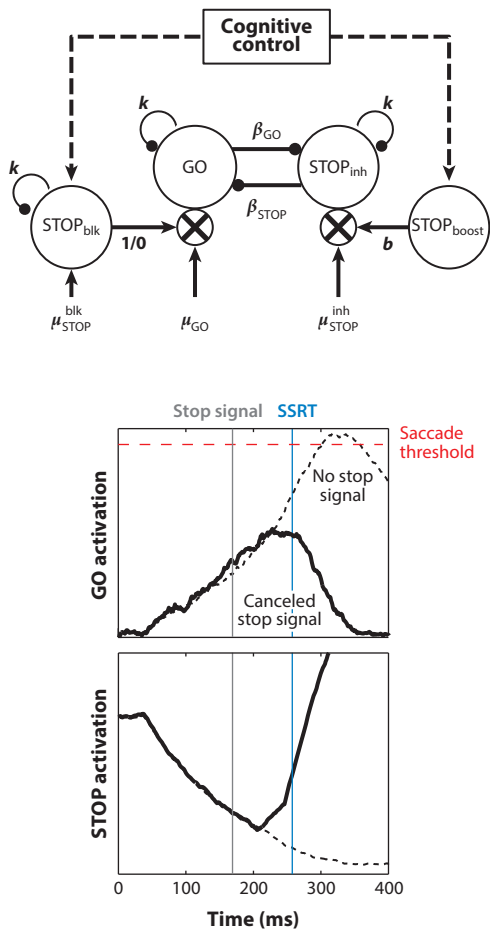


Figure 6

Interactive race model of saccade countermanding. The top panel diagrams the architecture of the circuit: Excitatory connections have arrowheads, and inhibitory connections have circle terminators. Activation of a GO unit, driven by an input (μ_{GO}), accumulates with leak (k) to specify whether and when a saccade will be initiated. A variety of alternative mechanisms can interrupt GO unit activation. All of these mechanisms instantiate delayed potent inhibition, allowing a network of interacting units to produce behavior that can be described as the outcome of a race between stochastically independent processes. Inhibition from a STOP unit (β_{STOP}) driven by an input (μ_{STOP}) can reduce activation of the GO unit, and this inhibition can be boosted by a cognitive control signal that potentiates the activation of the STOP_{inhibition} unit. Alternatively, activation of a STOP unit can interrupt or block the input to the GO unit. The inputs to the STOP_{block} (μ_{STOP}^{block}) and STOP_{inhibition} ($\mu_{STOP}^{inhibition}$) units are distinguished because they assume different values. These alternative architectures draw attention to the flexibility and adaptability of countermanding behavior afforded through cognitive control. The bottom panel illustrates the activation of the GO unit (*top plot*) and the STOP unit (*bottom plot*) for trials with no stop signal (*dashed lines*) and trials with a stop signal that successfully canceled the saccade (*solid lines*). Saccades are produced when inhibition of the STOP unit is released and the activation of a GO unit reaches a threshold (*dashed red line*). In response to the stop signal (*solid gray line*), the STOP unit becomes active, interrupting the accumulation of GO unit activation. This interruption occurs immediately before the stop signal reaction time (SSRT) (*blue line*), a measure of stop process duration derived from the independent race model. Figure adapted with permission from Logan et al. (2015).

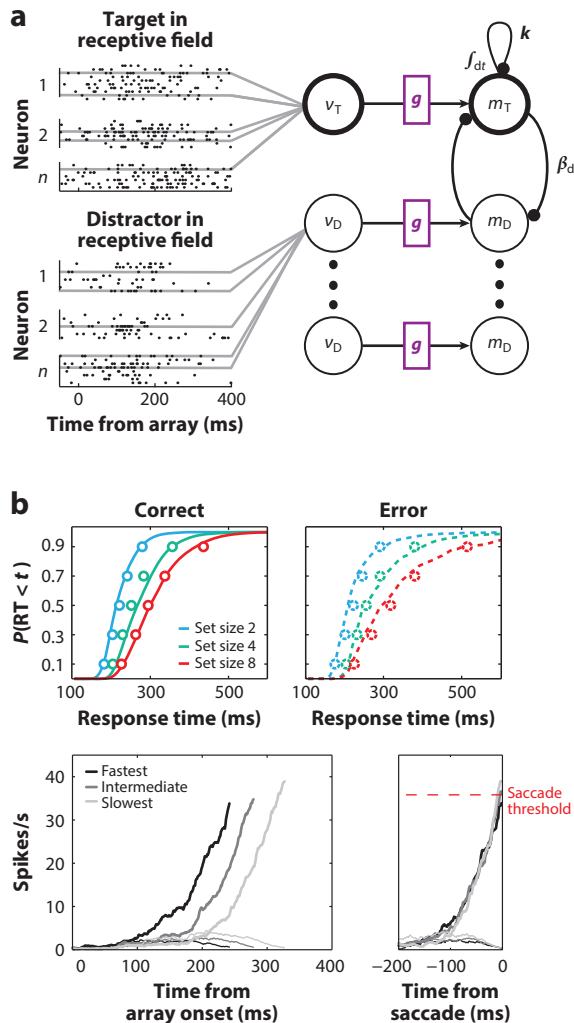


Figure 7

(a) Gated accumulator model of salience evidence accumulation. The diagram on the right shows the architecture of this circuit. Spike trains generated by frontal eye field (FEF) visual neurons representing object salience for target selection (in an array of input units v_T and v_D for a target and distractor, respectively). The evidence provided by the visual salience units is integrated by an array of accumulator units (m_T or m_D) with leak (k) and mutual inhibition (β). This array is separated from the input array by a gate (g) to prevent integration of noise; accumulation begins only after the gate is exceeded and target salience exceeds distractor salience. The direction and time of overt response were specified by the first accumulator unit to reach threshold.

(b) Graphs plotting performance (top) and replicated neural dynamics (bottom). The top plots show response times (RTs) in correct (left) and error (right) trials during visual search with set size 2 (blue), 4 (green), and 8 (red); circles represent data points, and lines represent model fits. The necessity of fitting details of performance provides powerful tests of model validity. The bottom plots illustrate the activation of the unit producing saccades to the target aligned on time from array presentation (left) and on time from saccade initiation (right) for the fastest, intermediate, and slowest subsets of RTs. The dynamics of the model unit, which corresponds functionally to the GO unit of the interactive race countermanding model, quantitatively replicate the modulation of presaccadic movement neurons in the FEF. Figure adapted with permission from Purcell et al. (2012a).

responses are recorded in both medial frontal areas (Pouget et al. 2005). SEF neurons are visually responsive, and they have receptive fields that are larger than those in the FEF with a more prominent ipsilateral representation (Schall 1991). The visual response latencies of SEF neurons are slower than those in the FEF and faster than those in the ACC (**Figure 2**), but visual neurons in the SEF can modulate well before temporally predictable visual stimuli (Coe et al. 2002). Neurons with enhanced and suppressed visual responses are found in all layers of the SEF, but, in response to a flash, early synaptic current sinks appear in L3 and L5, followed by a later sink in L2 (Godlove et al. 2014). Visually responsive neurons in the SEF do not participate in efficient saccade target selection (Purcell et al. 2012a); however, many appear to represent visual stimuli in object-centered coordinates (Moorman & Olson 2007).

The SEF was identified as a region at the rostral end of the SMA from which saccades can be elicited by electrical stimulation and in which neurons discharge in association with saccade production (Schlag & Schlag-Rey 1987, Schall 1991, Tehovnik et al. 2000). The human homolog of this area is similarly located (Amiez & Petrides 2009). The saccades elicited by SEF stimulation are of a different character than those elicited by FEF or SC stimulation; saccades elicited by SEF stimulation are produced in more reference frames (Martinez-Trujillo et al. 2004) and at many sites directed to a particular orbital position (Park et al. 2006). SEF projections overlap those of the FEF in the caudate nucleus, SC, and brainstem (Huerta & Kaas 1990, Shook et al. 1990, Parthasarathy et al. 1992). Eye movements can be elicited from a region in the dorsal area 24 cingulate motor areas (Mitz & Godschalk 1989). Inactivation of the SEF or ACC has minimal effects on saccade production in various tasks (Schiller & Chou 2000, Koval et al. 2014). Consistent with this, neural activity in the SEF does not directly control production of saccades (Stuphorn et al. 2010) or pursuit eye movements (Fukushima et al. 2006, Shichinohe et al. 2009). The SEF does contribute crucially to the production of sequences of saccades (Isoda & Tanji 2002, Lu et al. 2002, Histed & Miller 2006, Berdyeva & Olson 2010, Sharika et al. 2013). It also coordinates saccades with reaching (Fujii et al. 2002) and with head movements (Chen & Walton 2005, Chapman et al. 2012).

Thus, these medial frontal areas seem to be outside the direct visuomotor pathway. Rather, many other findings suggest that they can be understood as monitoring performance of tasks (Schall & Boucher 2007). The SEF contributes to abstract representations and dispositions that facilitate the performance of complex tasks (Amador et al. 2004, Moorman & Olson 2007, Stuphorn et al. 2010, Yang et al. 2010, Kunimatsu & Tanaka 2012) to a greater extent than the FEF does (Heinen et al. 2011, Middlebrooks & Sommer 2012, Yang & Heinen 2014). In addition, many studies have found that SEF and ACC neurons signal negative (error) and positive (reward) feedback (Amador et al. 2000, Stuphorn et al. 2000, Ito et al. 2003, Matsumoto et al. 2007, Uchida et al. 2007, Emeric et al. 2010, Kuwabara et al. 2014, So & Stuphorn 2012, Purcell et al. 2013, Shen et al. 2015). Such signals are likely the source of an ERP component known as the error-related and feedback-related negativity (Godlove et al. 2011, Phillips & Everling 2014) because it occurs after and is modulated by the conditions in which an error is performed (Gehring et al. 2012). The cerebral source of this error may be more extensive, though, as error signals have been described in the FEF (Teichert et al. 2014). Other neurons in the SEF—but not in the ACC—are modulated by conflict between competing responses (Stuphorn et al. 2000, Ito et al. 2003, Nakamura et al. 2005), an interesting contrast to human findings (Cole et al. 2009, Mansouri et al. 2009, Schall & Emeric 2010).

Performance adjustments based on these monitoring signals are accomplished through interactions with prefrontal areas and other structures. For example, subthreshold stimulation of the SEF improved performance of a saccade countermanding task by contingently increasing behavioral response time (Stuphorn & Schall 2006) that happens by delaying presaccadic movement activation in the FEF and SC (Pouget et al. 2011).

PREFRONTAL CORTEX

Primates possess an elaborate PFC, paralleled by expansions of parietal and temporal lobe areas that provide flexible behavior in complex and unpredictable foraging and social settings (Buckner & Krienen 2013, Genovesio et al. 2014, Pearson et al. 2014). The PFC consists of several areas, some of which are more clearly associated with visual behavior. Visually responsive neurons are found rostral to the FEF in area 8Ar, caudal area 46, area 45, and area 12, and these neurons are arranged according to a rough eccentricity map (Suzuki & Azuma 1983). Receptive fields tend to be in the contralateral hemifield, but a pronounced ipsilateral representation is also found, especially for tasks requiring a participant to select among stimuli in both hemifields (Everling et al. 2006, Lennert & Martinez-Trujillo 2013, Kadohisa et al. 2015). The collection of areas rostral to the FEF sends efferents to brainstem ocular motor circuits in parallel with the FEF (Borra et al. 2015).

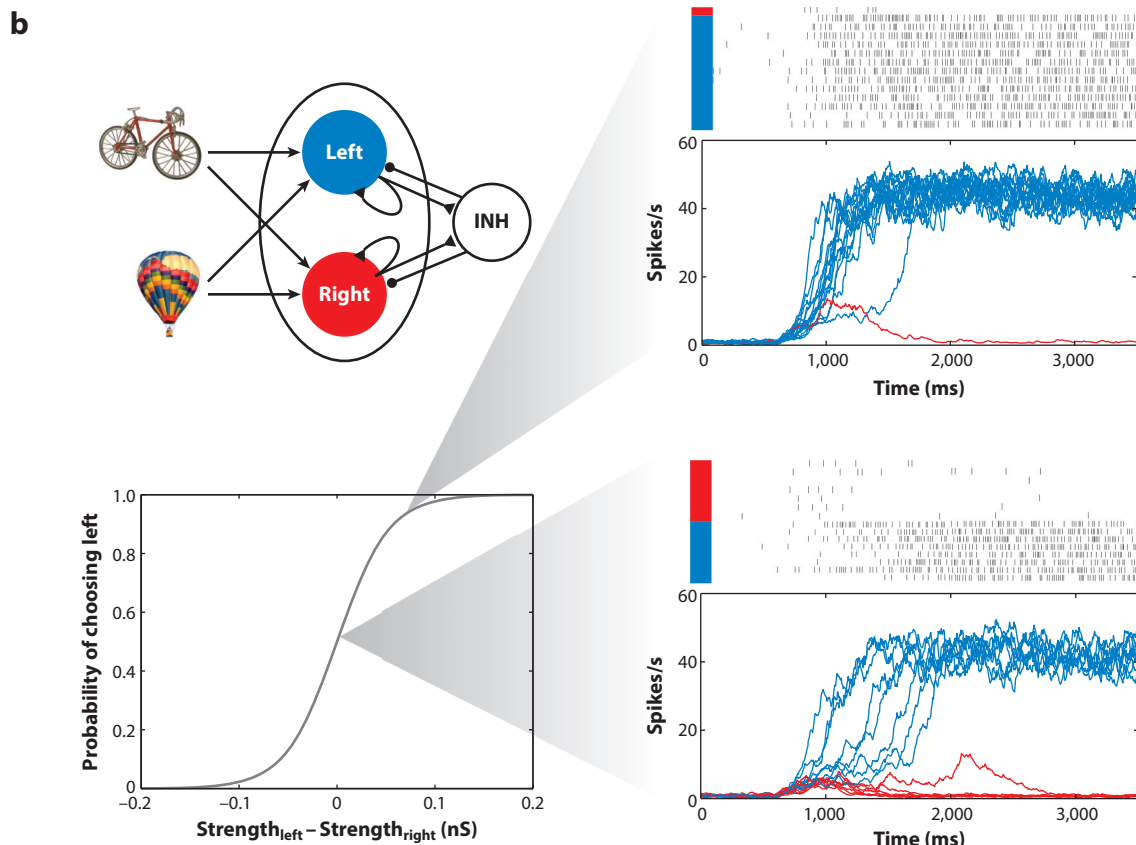
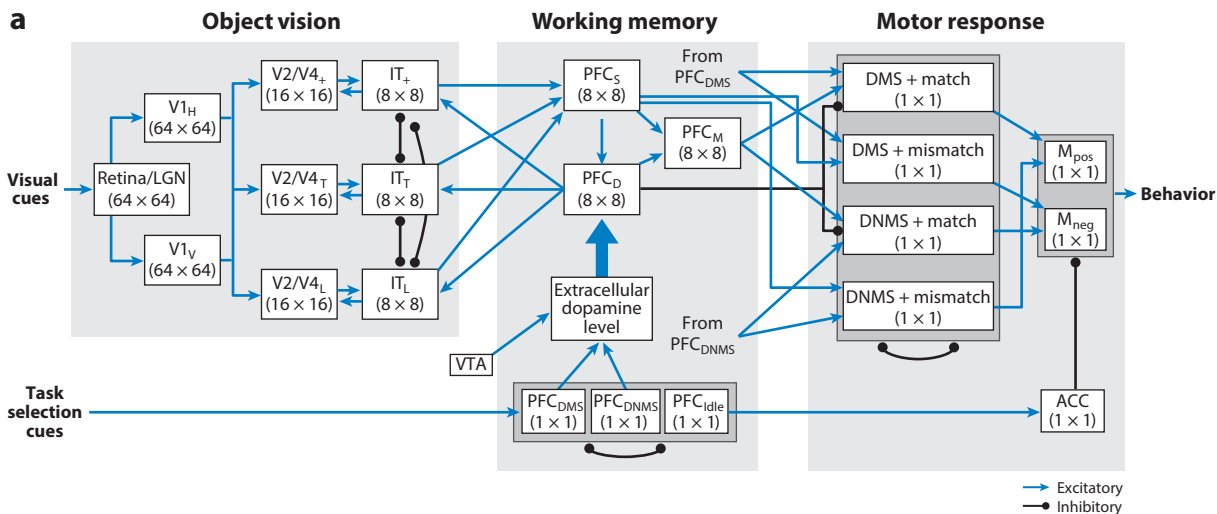
Many visually responsive neurons in the PFC sustain activity after a stimulus disappears if some feature of that stimulus must be remembered to perform a task; this sustained activity has been identified with working memory (Arnsten 2013; cf. Tsujimoto & Postle 2012, Sreenivasan et al. 2014). Consistent with the visual field map, the dorsal PFC tends to represent object location more than identity, whereas the ventral PFC tends to represent stimulus features or object identity; however, overlapping and mixed representations are common (Zaksas & Pasternak 2006, Meyer et al. 2011, Hussar & Pasternak 2013, Funahashi 2015, Kadohisa et al. 2015; cf. Lara & Wallis 2014).

The ventral PFC contributes to visual categorization performance (Roy et al. 2010, 2014; Seger & Miller 2010). Studies that compared the timing of categorization signals in prefrontal and parietal areas have had mixed results (Swaminathan & Freedman 2012, Crowe et al. 2013). Although these neural properties are present to some extent before training or even when monkeys are not performing a task, learning refines them and thereby enables performance of tasks requiring working memory for location, feature, or object category (Qi & Constantinidis 2013). Performance of such tasks is impaired by natural or experimental disruption of this sustained neural activity (Sawaguchi & Iba 2001, Zhou et al. 2013).

The PFC can represent and operate on abstract visual properties such as line length, proportions, and numerosity (Eiselt & Nieder 2013, Moskaleva & Nieder 2014); adapt to task demands (Warden & Miller 2010); and sustain signals necessary to maintain strategies, rules, and responses (Everling & DeSouza 2005, Johnston et al. 2007, Tsujimoto & Postle 2012). Many studies report neurons representing specific locations, features, objects, and task phases, but the advantages of multiplexed and flexible representations have been recognized (Messinger et al. 2009, Rigotti et al. 2013).

When presented with multiple stimuli in space or time, PFC neurons exhibit modulation in parallel with target selection and attention allocation. In spatial and object tasks, the selection time increases with target–distractor similarity (Kusunoki et al. 2010, Lennert & Martinez-Trujillo 2013, Kadohisa et al. 2013). Inactivation of the PFC impairs visual search performance (Iba & Sawaguchi 2003), especially when rules change (Rossi et al. 2007). As noted in the previous section, the PFC mediates performance adjustments to achieve goals (Mansouri et al. 2009, 2014). During attention allocation, and after errors, various interactions between medial and lateral frontal areas that could mediate executive control have been described (Shen et al. 2015, Womelsdorf et al. 2014).

The PFC influences saccade production through projections to the SC (Johnston & Everling 2009); these projections seem to ensure that gaze behavior conforms to task goals (Everling & Johnston 2013). One study has shown that inactivation of ventral area 46 impairs the ability



to generate prosaccades or antisaccades when the task rule is conveyed through reinforcement contingencies, but not when it is explicitly cued; inactivation of dorsal area 46 has no effect; and inactivation of both areas impairs overall ability to generate antisaccades (Hussein et al. 2014). Inactivation of area 46 in the principal sulcus reduces preparatory activity and increases visual responses of SC neurons in parallel with impairments in controlling saccade production guided by arbitrary cues (Koval et al. 2011).

Of course, none of these prefrontal functions happens without motivation and incentive. The orbitofrontal cortex (OFC) performs many functions, discussion of which is beyond the scope of this review (Zald & Rauch 2006). For visually guided behavior, the OFC endows stimuli with value via learned mapping to the nature of a reward in order to guide actions (Rolls & Grabenhorst 2008, Rushworth et al. 2012). For example, the selectivity of OFC neurons for faces may mediate rewarding social interactions (Rolls et al. 2006).

The diversity among observations about the PFC seems overwhelming. To synthesize the findings, neural network and biophysical models of PFC function have been formulated to explain the flexibility of sensorimotor mapping, selection and control of behaviors, and maintenance of working memory (**Figure 8**) (Machens et al. 2005, Chadderdon & Sporns 2006, Fusi et al. 2007, Pereira & Wang 2014). Further refinement of such models through iterative exclusion of alternative hypotheses should provide a more comprehensible account of the diversity of prefrontal functions.

MOTOR AND PREMOTOR CORTEX

We have considered how vision guides movements of the eyes, but vision also guides movements of the limbs. Neurons in the primary motor cortex respond to visual cues to guide movement (Liu et al. 2005, Rao & Donoghue 2014), but most research to date has focused on cue responses in the premotor cortex (Wallis & Miller 2003, Hoshi & Tanji 2006, Yamagata et al. 2009). The dorsal premotor cortex also contributes crucially to the coordination of eye, head, and limb movements

Figure 8

Models of prefrontal cortex (PFC) function for visually guided behavior. (a) A large-scale model embedding prefrontal functions with visual and motor functions to investigate how working memory and task state interact to select adaptive behaviors. The model consists of an object vision module (*left*), a working memory module (*center*), and a motor response module (*right*), which are used together to simulate performance of delayed match-to-sample (DMS) and delayed nonmatch-to-sample (DNMS) tasks. Numbers indicate how many units populate each modeled region. Each brain region is modeled with excitatory and inhibitory neurons having plausible physiological and anatomical properties. Blue arrows indicate excitatory connections, and circles indicate inhibitory connections. Three PFC layers represent the current stimulus (PFC_S), a remembered stimulus (PFC_D), and a match representation (PFC_M). Working memory is sustained through recurrent self-excitation and lateral inhibition among these layers, and these functions are modulated by the amount of dopamine released into the PFC. Such models usefully and systematically summarize a large body of data and simulate patterns of neural modulation, but they are either trivial or impossible to falsify, according to one's taste. Panel adapted with permission from Chadderdon & Sporns (2006). (b) A decision-making network. (*Top left*) Diagrams of the network architecture, including two excitatory subpopulations that are selective for the intended saccadic movements. The two populations compete through a group of inhibitory neurons (INH). The excitatory and inhibitory populations consist of integrate-and-fire neurons with plausible biophysical properties. Black arrows indicate the excitatory inputs activated by each visual stimulus. (*Bottom left*) Plot of the simulated probability that the left population wins over the right population, as a function of the difference in their respective activation strengths of representation; this function follows a sigmoidal curve (*gray line*). The panels on the right illustrate simulated raster plots (*top*) and spike density functions (*bottom*) for a single model neuron selective for left when left is chosen (*blue*) and right when right is chosen (*red*). When the activation strength of the left pool exceeds that of the right pool, left is chosen more often (*top*). When the synaptic inputs are balanced, left is chosen on half of the trials (*bottom*). Such models provide powerful platforms on which to explore how fundamental biophysical processes influence behavior; with so many free parameters, however, constraining such models to fit performance is difficult. Panel adapted with permission from Fusi et al. (2007).

(Batista et al. 2007, Pesaran et al. 2010) and to selection of reach targets during visual search (Song & McPeck 2010). In addition, a region in the rostral premotor cortex just caudal to the genu of the arcuate sulcus contributes somehow to the coordination of gaze and reaching (Fujii et al. 2000, Lebedev & Wise 2001).

In the ventral premotor cortex, the activity of some neurons modulates when the monkey executes a specific grasp action, as well as when the monkey observes the same action performed by another individual (Gallese et al. 1996; reviewed by Kilner & Lemon 2013). fMRI studies in humans have described activation in a homologous cortical region during observation of action (Molenberghs et al. 2012). Naming these mirror neurons and speculating about their role in social cognition have sparked incredible interest (e.g., Rizzolatti & Sinigaglia 2010).

The research group that first discovered these neurons (di Pellegrino et al. 1992) has obtained most of the subsequent neurophysiological data, but other laboratories have replicated and extended this finding to identify mirror neurons in M1 and parietal areas and have verified that some mirror neurons have corticospinal projections (e.g., Kraskov et al. 2009, Dushanova & Donoghue 2010, Kilner et al. 2014). The name “mirror neuron” conceals a diverse group of response properties. Some of these neurons respond to video action, but some require actual action. Some are selective for particular actions, points of view, or goals. Some are active during execution of a movement and suppressed during observation of that movement. One invasive recording study has reported mirror neurons in humans (Mukamel et al. 2010); curiously, these neurons were found in the SMA and in the hippocampus, but the ventral premotor cortex could not be investigated. The empirical gap separating the macaque neurophysiological findings from the human brain imaging findings is being bridged in several ways. First, fMRI activation in response to action observation has been reported in the premotor cortex of macaque monkeys (Nelissen et al. 2011). Second, the reduction of the fMRI response following repeated presentations of a stimulus has been employed to identify mirror neurons, although the results have been mixed (Dinstein et al. 2007, Lingnau et al. 2009), perhaps because mirror neurons recorded in monkeys adapt little if at all in response to repeated stimulus presentations (Kilner et al. 2014, Caggiano et al. 2013). Clearly, this fascinating feature of the premotor cortex deserves further research, leavened with healthy skepticism (Jacob & Jeannerod 2005).

CONCLUDING QUESTIONS

Hopefully the reader is as impressed as the author is by the progress made in understanding how vision becomes action in the frontal lobe. Let us conclude with a list of questions for further research while noting more comprehensive surveys of the frontal lobe (Fuster 2008, Passingham & Wise 2012).

First, how important are the specificity and distinctiveness of areas, circuits, and cells? Some studies find elaborate specificity (e.g., Gregoriou et al. 2012); others emphasize generality (e.g., Mante et al. 2013, Rigotti et al. 2013). For perspective, our understanding of the retinogeniculo-cortical pathway was established by identifying the distinct classes of cells, circuits, and areas. The search for corresponding specificity in the frontal lobe will be equally informative (e.g., Ardid et al. 2015); however, that search cannot overlook the flexibility of the frontal lobe in adapting to the vicissitudes of environment and experience.

Second, how effectively will knowledge about occipital circuitry translate into understanding of frontal circuitry? Some researchers have applied the canonical cortical microcircuit derived from the primary visual cortex to frontal areas (e.g., Heinzle et al. 2007), but there are clear differences in cortical architecture and organization between occipital and frontal areas (e.g., Elston 2003, Ninomiya et al. 2015). Indeed, without a dense granular L4, how can the visual cortex circuitry

apply to the motor cortex (Shipp 2005)? Further research will reveal whether the similarities or the differences are more important.

Third, how effectively will findings translate between species? Although many homologies of macaque and human cortical organization have been described (e.g., Petrides et al. 2012), we must remember that humans do have cognitive and behavioral abilities beyond those of other primates. Meanwhile, other researchers are describing the rodent PFC (e.g., Kesner & Churchwell 2011), motivated by opportunities for experimental manipulations currently unavailable to researchers working with primates. Although investigation of the rodent frontal cortex will no doubt be a productive research area, we must not overlook the fundamental differences between rodents and primates in life span, habitat, behavioral ecology, and cortical organization (e.g., Passingham & Wise 2012, Preuss 2000, Gabi et al. 2010). Such differences can explain the limited translation of rodent findings to human therapy (e.g., Bolker 2012).

Fourth, does the frontal lobe have a unitary function? Probably not—to say the occipital lobe does vision falls very short of all we know. And, no area is an island (e.g., Markov et al. 2014), so any satisfying account of frontal lobe function must explain how signals from extrastriate visual areas are combined and selected to guide movements and how the frontal lobe influences processes in the back and in the bottom of the brain.

Finally, how can frontal lobe function be understood without using psychologically useful but scientifically ambiguous terms such as attention, decision, memory, plan, rule, goal, or value, among others? Progress depends on replacing vague prolix with computationally and biophysically precise mechanistic models that give a homunculus nothing to do and nowhere to hide in the frontal lobe. Of course, as these models are successively refined, the particularities of the primate frontal lobe and primate cognition and behavior will become more evident and important. Ultimately, the complexity of the frontal lobe may discourage the theorist, but it should satisfy the psychologist and delight the biologist.

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Errata

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