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Frontal Eye Fields

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Without Abstract

Definition

Frontal eye field (FEF) is the area in dorsolateral prefrontal cortex that signals the location of targets and controls the execution of goal-directed movements of the eyes.

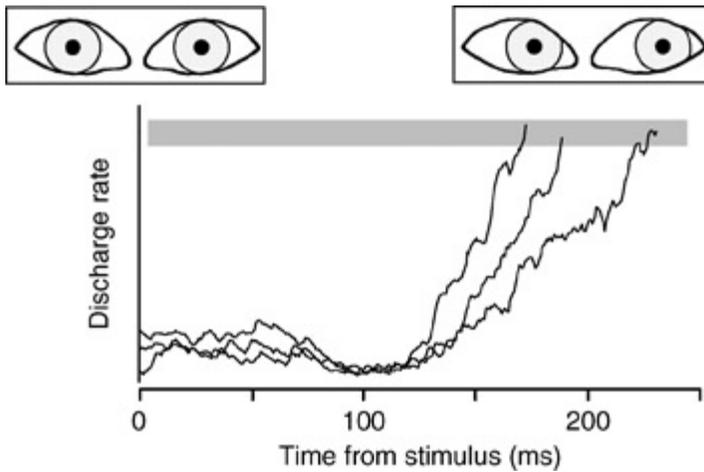
Characteristics

Higher Level Structures

FEF influences *saccade* production through three pathways – a projection to the ipsilateral superior colliculus concentrated in the intermediate layers, a pathway through the basal ganglia via the ipsilateral striatum and subthalamic nucleus, and a projection to mesencephalic and pontine nuclei [1].

FEF is innervated by nuclei in the thalamus bordering the internal medullary lamina, mainly the lateral part of the mediodorsal nucleus and the medial part of the ventroanterior nucleus. The thalamic zones most heavily connected with FEF are themselves innervated by oculomotor afferents from the intermediate layer of the superior colliculus, the substantia nigra pars reticulata, and the dentate nucleus of the cerebellum.

FEF is connected with diverse cortical areas. Within the frontal lobe FEF is interconnected with SEF, with prefrontal areas 46 and 12, and weakly with anterior cingulate area 24 and postarcuate premotor cortex. FEF also receives abundant inputs from a multitude of visual cortical areas in both the dorsal and ventral streams [2]. In fact, FEF is unique in the extent of its connectivity with extrastriate visual cortex, and it should not be overlooked that FEF provides reciprocal connections to equally many extrastriate visual areas. Thus, FEF can influence the activation of neurons in extrastriate visual cortex.

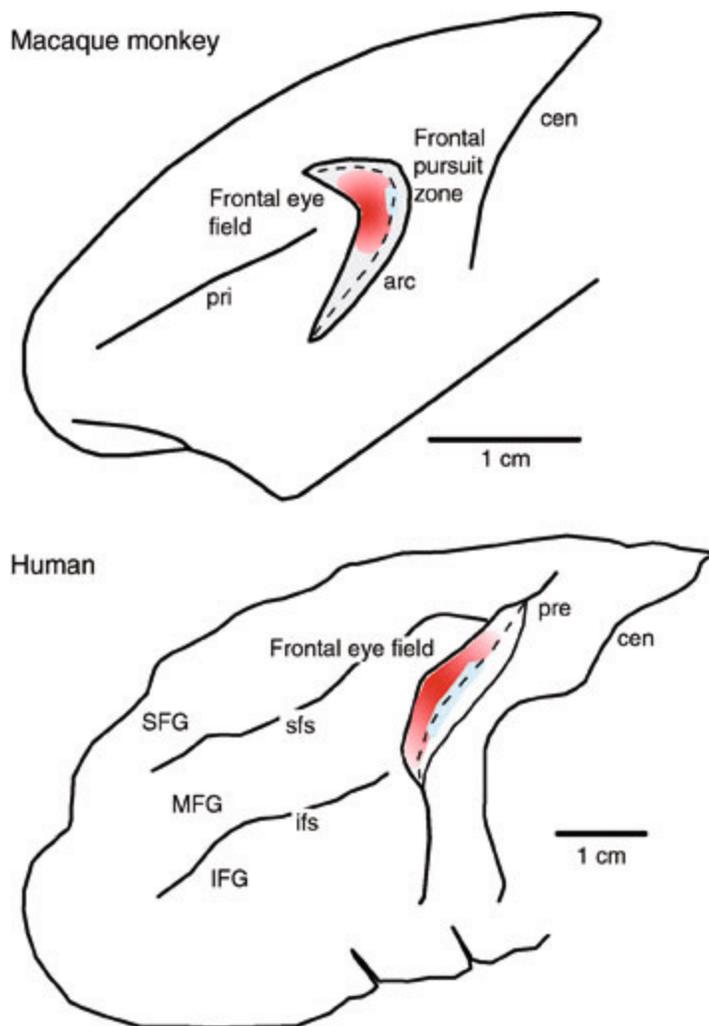


Frontal Eye Fields. Figure 2 Saccades are produced when the activity of movement-related neurons in frontal eye field, as part of a network, reach a fixed threshold. Variability in the time of initiation of the saccade originates in the variable time taken for the activity to increase to the threshold.

The connectivity of FEF with visual areas caudal to the central sulcus is topographically organized. The more ventrolateral portion of FEF, which is responsible for generating shorter saccades, is interconnected with the perifoveal representation in retinotopically organized areas, from areas that represent central vision in inferotemporal cortex and from other areas having no retinotopic order. In contrast, mediodorsal FEF, which is responsible for generating longer saccades, is interconnected with the peripheral visual field representation of retinotopically organized areas, from areas that emphasize peripheral vision or are multimodal and from other areas that have no retinotopic order.

Lower Level Components

In macaque monkeys, FEF occupies the rostral bank of the arcuate sulcus in Brodman's area 8 (Fig. 1). At a more refined level, the dorsal part of the rostral bank is designated area 8Ac and is distinguished from area 45 in the lower limb of the arcuate sulcus. The lip and convexity of the rostral bank of the arcuate sulcus is designated area 8Ar which borders rostrally with area 46. In humans, FEF is located in the rostral bank of the precentral sulcus at the caudal end of the middle frontal gyrus (Fig. 1). However, human FEF has been described as being in Brodman's area 6. The apparent difference between species seems to be more a difference of labels than of cortical architecture.



Frontal Eye Fields. Figure 1 Stylized, lateral view of frontal cortex of macaque monkey (*top*) and human (*bottom*). The macaque arcuate sulcus is opened to expose the frontal eye field (red) on the rostral bank and the frontal pursuit zone (blue) on the fundus. The human precentral sulcus is opened to expose the frontal eye field (red) on the caudal end of the middle frontal gyrus with the pursuit zone (blue) in the fundus. Abbreviations: *arc*, arcuate sulcus; *cen*, central sulcus; *IFG*, inferior frontal gyrus; *ifs*, inferior frontal sulcus; *MFG*, middle frontal gyrus; *pre*, precentral sulcus; *pri*, principal sulcus; *SFG*, superior frontal gyrus; *sfs*, superior frontal sulcus.

Higher Level Processes and Lower Level Processes

Role in Eye Movement Generation

The FEF has been regarded most commonly as part of the ocular motor system; the evidence for this is beyond dispute [1]. Most evidence has been obtained through invasive studies with nonhuman primates, but the human FEF has been located through brain imaging [3], transdural recording and stimulation [4], and transcranial magnetic stimulation [5]. FEF contributes to the generation of rapid saccadic gaze shifts as well as slow pursuit eye movements. The zone involved in pursuit is located at the fundus of the sulcus, separate from the area of frontal eye field that is involved in saccade production (Fig. 1).

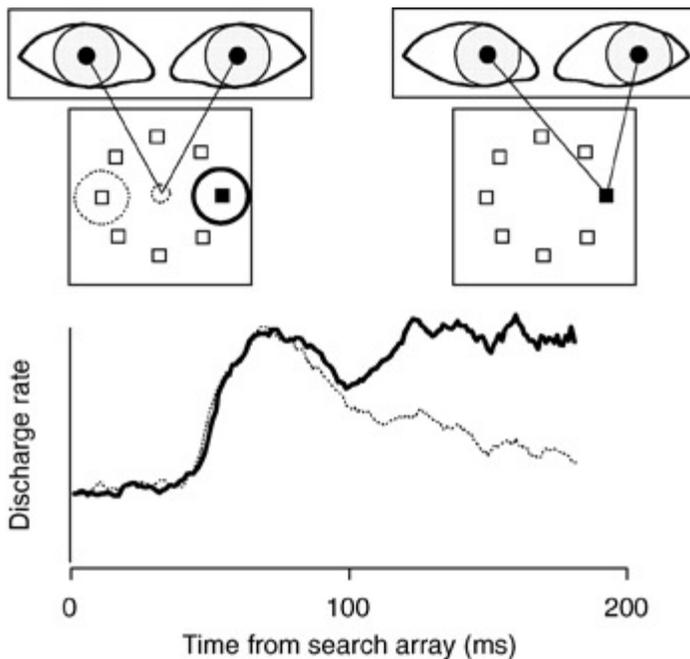
Low intensity electrical stimulation of FEF in monkeys elicits saccadic eye movements, while stimulation of the **frontal pursuit area** elicits pursuit eye movements. Reversible inactivation of FEF prevents saccade production, complementing earlier observations that ablation of FEF causes an initially

severe impairment in saccade production that recovers in some but not all respects over time. If the fundus of the arcuate sulcus is ablated, pursuit deficits occur.

The direct influence of FEF on saccade production seems to be mediated by neurons in FEF that are activated specifically before and during saccades [6,7]. Two kinds of neurons that control gaze have been distinguished. In general, *movement* neurons contribute to gaze shifting, and *fixation* neurons contribute to gaze holding. Neurons in FEF that generate movement-related or fixation-related activity are located in layer 5 and innervate the superior colliculus and parts of the neural circuit in the brainstem that generate saccades. Physiological recordings indicate that these neurons, in concert with a network including the superior colliculus, produce signals necessary to produce saccadic eye movements. Saccades are initiated when the activity of movement-related neurons reaches a threshold (Fig. 2). Variability in saccade latency can be accounted for by the time taken to reach this threshold. If an interrupting stimulus occurs, saccade preparation is canceled if, and only if, the activity of these neurons is reduced and prevented from reaching the threshold.

Role in Target Selection

FEF contributes to selecting the target and shifting attention before gaze shifts, both saccadic and pursuit [8]. It is also crucial to note that the neural signals occurring in FEF coincide with identical signals occurring in a network of interconnected structures including the superior colliculus and posterior parietal cortex. In macaque monkeys trained to shift gaze to the oddball target in visual search arrays, most visually responsive cells in FEF responded initially indiscriminately to the target or the distractor of the search array in their receptive field because neurons in FEF are not feature selective (Fig. 3). However, before gaze shifts, a selection process transpires by which most visually responsive cells in FEF signal the location of the target stimulus through suppression of the response to non-target stimuli, leaving only the response to the target. This selection process occurs if no saccade is made or if the saccade is directed to a non-target stimulus. The selection process is influenced by the similarity of the target and non-target stimuli, taking longer the more similar the stimuli. The selection process is also influenced by knowledge of target properties acquired over preceding trials or sessions. These properties of the target selection process observed in FEF indicate that it can be identified with the allocation of visual spatial attention. The contribution of FEF and surrounding cortex to the allocation of spatial attention has been described in human studies using functional brain imaging [9] and transcranial magnetic stimulation [10]. All of these data can be organized under the framework that FEF is a salience map.



Frontal Eye Fields. Figure 3 Targets for saccades are selected by the pattern of activity of visual neurons in frontal eye field, as part of a network. The activity of a visual neuron of a monkey shifting gaze to a single conspicuous stimulus. The response to the target (solid line), and the response to a distractor (dotted line), are superimposed for comparison. The stimulus array is shown at the top with superimposed receptive fields mapping onto the corresponding activation. After around 100 ms a selection process transpires that results in an accurate representation of the location of the target that can be used to guide the saccade.

Function

The FEF as part of a network samples the outcome of sensory processing to orient toward conspicuous and important elements in the environment.

Pathology

Damage to the area of cortex including the FEF in humans results in deficits in controlling gaze in response to arbitrary cues while leaving visually guided eye movement control largely intact.

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