Encyclopedia of Neuroscience
Springer-Verlag GmbH Berlin Heidelberg 2009
10.1007/978-3-540-29678-2_5765
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Supplementary Eye Field

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Without Abstract

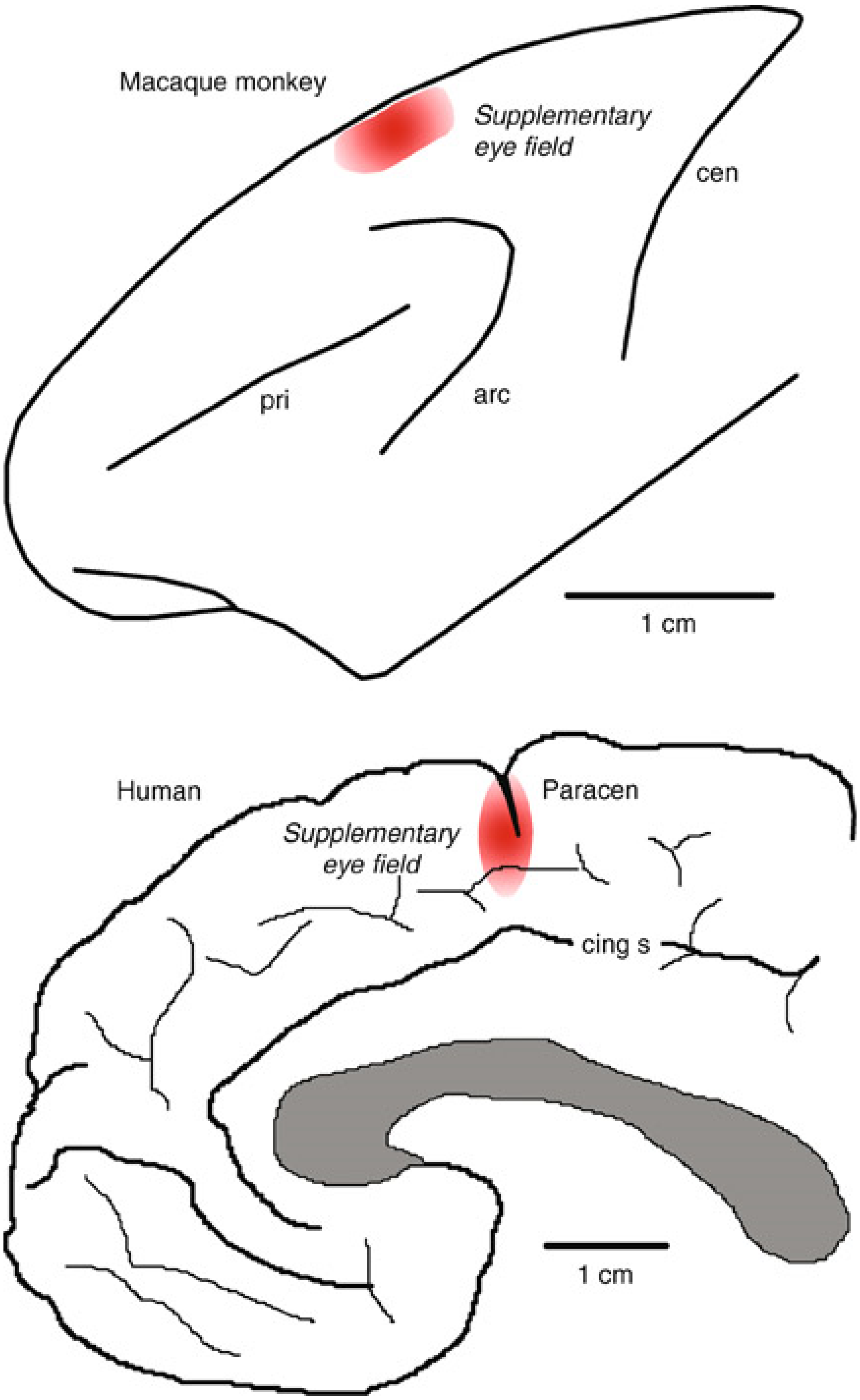
Definition

The supplementary eye field (SEF) is an area in the dorsal medial frontal lobe of the cerebral cortex that contributes indirectly to the control of movements of the eyes.

Characteristics

Higher Level Structures

SEF is located at the rostral end of the supplementary motor area, contiguous with the representation of orofacial, pinna and forelimb movements. SEF is located in Brodman's area 6 and corresponds to area F7 [*1*]. The human SEF is located on the medial surface of the superior frontal gyrus in the upper part of the paracentral sulcus (Fig. 1).



Supplementary Eye Field. Figure 1 Location of supplementary eye field in lateral view of frontal lobe of macaque monkey (*top*) and medial view of frontal lobe of human (*bottom*). In macaque monkeys, SEF is located on the dorsomedial convexity, medial to the upper limb of the arcuate sulcus. In humans, SEF is located dorsally on the medial surface around the paracentral sulcus. Abbreviations: *arc*, arcuate sulcus; *cen*, central sulcus; *cing s*, cingulate sulcus; *pri*, principal sulcus.

Lower Level Components

The connectivity of SEF is distinct from that of the skeletal motor cortex surrounding it, and SEF shares many but not all efferent targets and afferent sources with the frontal eye field (FEF) [2,3]. The major thalamic inputs to SEF arise mainly from the medial ventroanterior nucleus and the lateral segment of the mediodorsal nucleus as well as the intralaminar thalamic nuclei. These thalamic inputs convey signals mainly from the visuomotor zone of the substantia nigra pars reticulata, the intermediate layers of the superior colliculus and the face representation of the deep cerebellar nuclei. SEF projects to the caudate nucleus in a zone largely but not completely overlapping afferents from FEF, to the superior colliculus in a more diffuse pattern than the FEF counterpart, to specific brainstem oculomotor regions such as the nucleus raphe interpositus, the nucleus reticularis tegmenti pontis, the nucleus prepositus hypoglossi, the mesencephalic reticular formation, the interstitial nucleus of Cajal and the pontine reticular formation as well as the dorsomedial pontine nuclei.

SEF is reciprocally connected with several cortical areas, although fewer visual areas than is FEF. SEF interacts directly with area MST, the superior temporal polysensory area, area LIP, with anterior and posterior cingulate cortex and with the postarcuate premotor areas as well as the supplementary motor area and with prefrontal cortex in areas 12 and 46. SEF is also heavily connected with FEF in a spatial pattern that departs from the typical topography observed between other cortical areas.

Higher Level Processes and Lower Level Processes

Sensory Processes

Neurons in SEF respond to visual and auditory stimuli [2,3]. However, visual responses are later and less vigorous than those observed in FEF. SEF neurons exhibit various kinds of extraretinal modulation including anticipatory activity and responses conditional on stimulus-response mapping rules [4]. Thus, SEF visual responses reflect less about the properties of the image and more about the stimulus in the context of the ongoing behavior.

Gaze Control

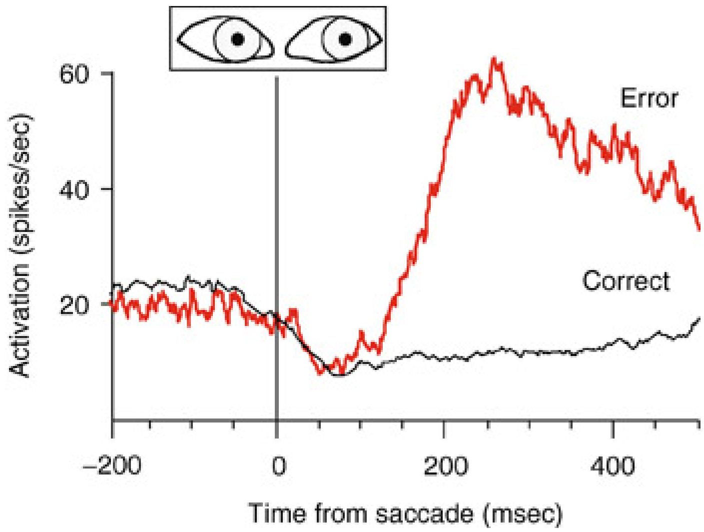
A great deal of evidence demonstrates that the SEF plays some role in the production of movements of the eyes [2,3]. In his pioneering electrical stimulation studies in humans, Penfield noted gaze shifts evoked by stimulation of the rostral part of the supplementary motor area (SMA). This finding has been confirmed using subdural electrode arrays to stimulate and record in humans. Schlag and Schlag-Rey first identified SEF as an area in which low intensity microstimulation evokes saccades and neurons discharge in relation to saccade production [5]. SEF neurons are also active in relation to the production of pursuit eye movements [6].

Numerous functional brain imaging studies using PET and fMRI have described activation in and around SEF of humans producing saccades [7]. Common findings include greater activation in SEF associated with antisaccades or memory-guided saccades relative to simple visually guided saccades.

Several other characteristics of SEF distinguish it from FEF. Electrical stimulation of many sites in SEF evokes saccades with dimension and direction dependent on the position of the eyes in the orbit, unlike what is observed in FEF or superior colliculus. Also, the saccade-related activity of many SEF neurons is contingent on the context in which the saccade is produced. Finally, despite the apparent relation of SEF to saccade production, when tested in a task requiring control of saccade initiation, few neurons in SEF generate signals that are sufficient to control gaze. Thus, although anatomically and physiologically SEF seems to parallel FEF in many respects, SEF seems to play a less essential or potent role in saccade production.

Supervisory Control

Diverse more complex functional properties of SEF neurons have been described including conditional motor learning, object-centered representation, production of anti-saccades and sequences of saccades and eye-hand coordination. Theories of executive control cite five types of behavior that require supervisory control – planning or decision making, error correction, producing responses that are not well-learned, dealing with difficult or risky conditions and overcoming habitual responses. These categories include the conditions under which various investigators have reported neural activity in supplementary eye field. Therefore, these diverse findings can be organized under the hypothesis that SEF is part of a supervisory control network that is called into action when alternative responses are difficult to distinguish, habitual responses must be overcome, consequences are uncertain, and deliberation is necessary [*8*,*9*]. The supervisory system exerts control over the processes that produce sensory-guided movements. Physiological evidence for a supervisory system in humans includes a scalp potential referred to as the error-related negativity that occurs when subjects produce errors. In macaque monkey SEF, certain neurons exhibit modulation specifically following a saccade that is an error (Fig. 2). Other neurons in SEF signal the anticipation and receipt of reinforcement. Still other neurons in SEF seem to signal the amount of mutually incompatible co-activation occurring. Error, reward and conflict signals form the basis of current models of executive control. Therefore, the most plausible current hypothesis about the function of SEF proposes that it provides executive control when saccades are produced under complex conditions.



Supplementary Eye Field. Figure 2 Activity of a representative SEF neuron aligned on the initiation of a saccade that was correct (black) and an error (red). This neuron signaled the production of errors.

Function

SEF contributes to the executive control of eye movements.

Pathology

Damage to SEF in humans or monkeys results in symptoms that are relatively mild and difficult to discern. Experimental ablation or inactivation of the SEF in macaque monkeys does not impair accurate fixation of eccentric visual targets or execution of saccadic eye movements to single visible or to remembered target locations. Modest impairment in production of sequences of saccades is observed. Transcranial magnetic stimulation that transiently inactivates SEF in humans also impairs production of a memorized sequence of eye movements. It should be noted that combined ablation of the FEF and the superior colliculus, leaving the SEF intact, produces effective gaze paralysis. These observations reinforce the conclusion that SEF plays an indirect role in gaze control. A recent report of one patient with a lesion restricted to SEF in one hemisphere described impaired self-control but intact error monitoring during a saccade task.

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