Exp Brain Res (1985) 58: 208–211

Experimental Brain Research

© Springer-Verlag 1985

Research Note

Unit activity related to spontaneous saccades in frontal dorsomedial cortex of monkey

J. Schlag and M. Schlag-Rey

Department of Anatomy and Brain Research Institute, University of California, Los Angeles, CA 90024, USA

Summary. Single unit activity was studied in the dorsomedial edge of the frontal lobe, above the superior arcuate sulcus in three trained monkeys (Macaca nemestrina). Gaze and head movements were recorded with two magnetic search coils. Discharges preceding spontaneous eye movements in a preferred direction were consistently observed in light and in dark, in a limited cortical territory at the anterior border of the supplementary motor area. Microstimulation at these sites elicited saccades in the unit preferred direction. Five presaccadic units were studied head fixed and head free and showed the same saccade-related activity under both conditions. Preliminary data suggest that the area studied may be a supplementary eye field distinct from the arcuate frontal eye field.

Key words: Supplementary eye field – Presaccadic discharges – Spontaneous saccades – Dorsomedial frontal cortex

As the participation of different cerebral structures in the guidance of the gaze becomes better understood, one puzzling question still remains: what role, if any, does the cortex play in the generation of self-initiated, purposive eye movements?

Most of our knowledge of cortical gaze mechanisms is derived from single unit studies made in two areas, the posterior parietal lobe and the arcuate frontal eye field. In both areas, neuronal activity seems contingent on the presence of visual stimuli; it does not occur with spontaneous saccades (Bizzi 1968; Mountcastle et al. 1975). Reexamining the problem recently, Bruce and Goldberg (1985) verified that the natural condition for presaccadic discharges in arcuate neurons is the performance of a task in which the target of eye movements is signalled by visual cues; with no task the same neurons do not fire or fire very little for comparable saccade vectors. For all muscles in the body, there are cortical neurons which discharge prior to the onset of movements in a manner consistent with the hypothesis that they drive these movements, whether spontaneous or not. Either extraocular muscles constitute an exception to this rule – implying that the control of spontaneous saccades is entirely subcortical – or the cortical neurons participating to this control have not yet been identified. As saccades are quite often self-initiated for the purpose of exploring, i.e. a complicated operation involving voluntary decisions on where and when to look, any hypothesis excluding cortical mechanisms in their generation seems implausible.

Recently, we probed with microelectrodes the frontal dorsomedial cortex of monkeys in order to detect neuronal activity possibly related to the generation of saccades outside the arcuate frontal eye field (FEF). This project was prompted by three considerations: the existence of a medial FEF in cat (Schlag and Schlag-Rey 1970), of an oculomotor zone attached to the supplementary motor area (SMA) as mapped by Woolsey et al. (1952) in monkey, and of anatomical projections from frontal dorsomedial cortex to the superior colliculus (Leichnetz 1980), and the region of the oculomotor complex (Leichnetz et al. 1984). Later on, it came to our attention that some SMA units had been described as related "to some aspects of vision or movements of the eyes" (Brinkman and Porter 1979). Our experiments were done in three alert Macaca nemestrina trained in visual tasks providing instances of visually triggered saccades, saccades of retargeting, and spontaneous

---

Offprint requests to: J. Schlag, Department of Anatomy, Medical School, University of California at Los Angeles, Los Angeles, CA 90024, USA

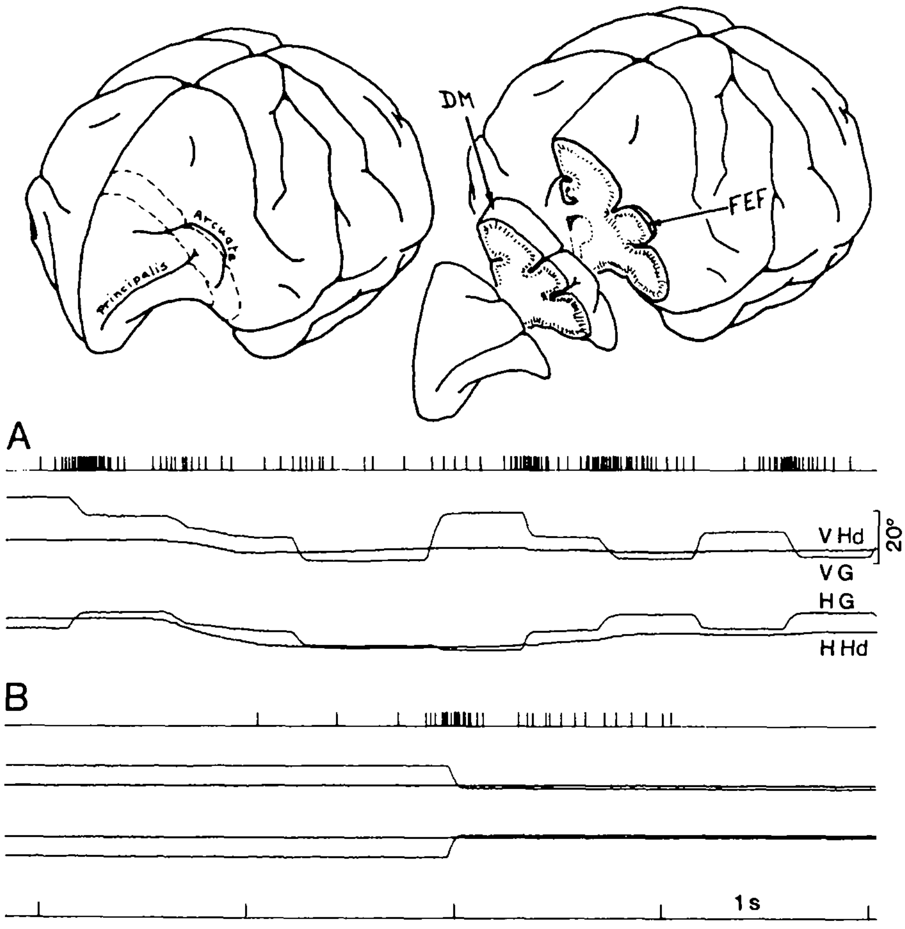

Fig. 1A and B. At top, front-left views of monkey's brain showing relative positions of dorsomedial cortex (DM) and arcuate frontal eye field (FEF). **A** and **B** Dorsomedial presaccadic unit recorded head free. VG – vertical gaze; VHd – vertical head; HG – horizontal gaze; HHd – horizontal head; upward deflection means toward right. Unit was firing with down-right saccades. Isolated saccade when head was still in **B**

saccades. Eye movements were recorded with a scleral search coil.

Units active with spontaneous saccades in light and in dark were isolated in a restricted ($\simeq$ 5 mm^2) region of the dorsomedial edge of the superior frontal convolution, at the antero-posterior level of the superior arcuate sulcus. This area of agranular cortex, corresponding to the Vogt's area 6aβ (marked DM in Fig. 1), is clearly separated by about 10 mm from the classical frontal eye field (FEF). Records were obtained from 18 postsaccadic and 62 presaccadic units. Among the latter, many started discharging as long as 500 ms before spontaneous saccades. Typically, the firing increased gradually, as shown in Fig. 2, to culminate at the time of the movement. The profile of unit activity was thus reminiscent of the time course of the d.c. Bereitschaftspotential as it develops over the vertex preceding saccades in humans (Becker et al. 1972). About 80% of the presaccadic units had a clear direction preference: they discharged only or more strongly before saccades directed to one side, usually contralateral. Possible relations of the firing with saccade size and site of termination are now under investigation.

Electrical stimulation through the microelectrodes at the sites of recording presaccadic units always evoked saccades in the unit preferred direction. The latencies of response varied from 45 to 90 ms depending on the site and current used. The threshold current usually was 20 to 50 μA (minimum: 4 μA obtained in six cases) using 0.2 ms cathodal pulses at 250 Hz. But such low currents were effective only very locally. When stimulation was applied systematically every 0.5 mm without the guidance of preliminary unit recording, thresholds were almost always above 50 μA.

Since the results of some early stimulation studies (e.g. Brown 1922) suggest that the superior frontal convolution is concerned primarily with head rather than eye movements, we had to consider the possibility that the unit activity recorded there was related to attempted head movements rather than being truly presaccadic. Attempted head movements are not

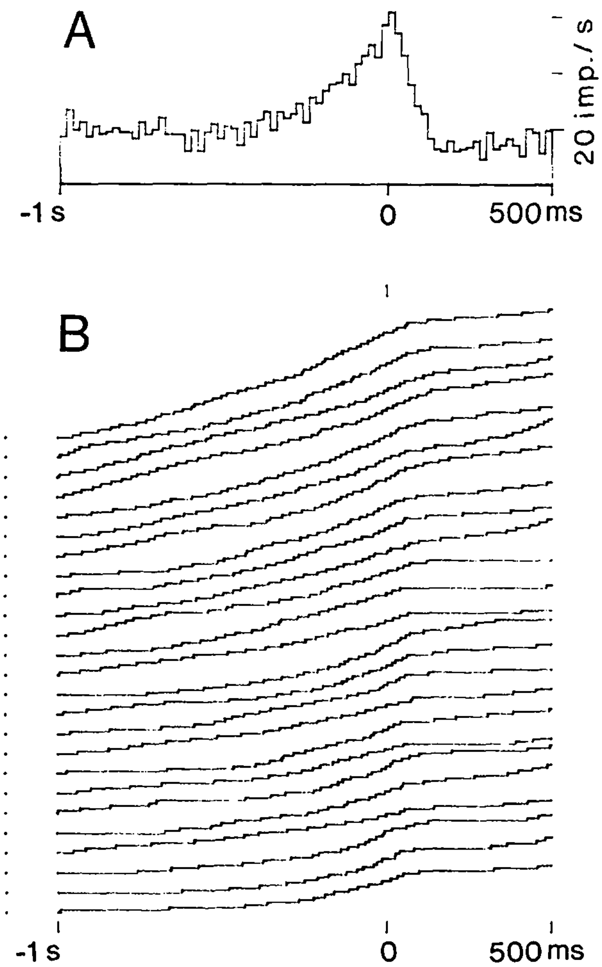

Fig. 2A and B. Unit increasing its firing rate before downward spontaneous exploratory saccades. **A** Peri-saccadic histogram, saccade onset at time zero. **B** Cumulative plot of impulses showing that progressive acceleration of firing is noticeable in individual trials as well as in the average

observable when the head is restrained, yet neck EMG readings have shown them to accompany saccades (Lestienne et al. 1984) and, eventually, to start before them. For this reason, we released the monkey's head during a few sessions. Gaze and head positions were continuously recorded with independent search coils. Five presaccadic units first observed head fixed continued to show the same relation with saccades irrespective of head movements (Fig. 1). Stimulation at these sites elicited isolated saccades with no head movements, even when the current was doubled or the train duration was increased to 1 s.

Other observations were made in these preliminary experiments: for instance, regarding the existence of visually responsive units (N = 113). But the purpose of this note is essentially to report the involvement of the dorsomedial frontal cortex in the initiation of spontaneous saccades. In fact, some units were active exclusively with spontaneous saccades, not with visually triggered ones.

The results are consistent with changes of d.c. potential (Becker et al. 1972) and changes of regional cerebral blood flow (Orgogozo and Larsen 1979) recorded with saccades over the vertex in humans. Clinical observations indicate that the SMA plays a major role in spontaneous voluntary movements including speech (e.g. Rubens 1975; Laplane et al. 1977; Kirzinger and Jürgens 1982; Libet et al. 1983; Jürgens 1984). In contrast, movements elicited by stimuli remain relatively unimpaired. The present results suggest that the dorsomedial cortical area studied could be a "supplementary eye field".

Acknowledgement. This research was supported by USPHS grant NS4955.

References

Bizzi E (1968) Discharge of frontal eye field neurons during saccadic and following eye movements in unanesthetized monkeys. Exp Brain Res 6: 69–80

Becker W, Hoehne O, Iwase K, Kornhuber HM (1972) Bereitschaftspotential, prämotorische Positivierung und andere Hirnpotentiale bei sakkadischen Augenbewegungen. Vision Res 12: 421–436

Brinkman C, Porter R (1979) Supplementary motor area in the monkey: activity of neurons during performance of a learned motor task. J Neurophysiol 42: 681–709

Brown TG (1922) Reflex orientation of the optical axes and the influence upon it of the cerebral cortex. Arch Neerl Physiol 7: 571–578

Bruce CJ, Goldberg ME (1985) Primate frontal eye fields; I. Single neurons discharging before saccades. J Neurophysiol (in press)

Jürgens U (1984) The efferent and afferent connections of the supplementary motor area. Brain Res 300: 63–81

Kirzinger V, Jürgens V (1982) Cortical lesion effects and vocalization in the squirrel monkey. Brain Res 233: 299–315

Laplane D, Talairach J, Meininger V, Bancaud J, Orgogozo JM (1977) Clinical consequences of corticectomies involving the supplementary motor area in man. J Neurol Sci 34: 301–314

Leichnetz G (1980) An anterogradely-labeled prefrontal cortico-oculomotor pathway in the monkey demonstrated with HRP gel and TMB neurochemistry. Brain Res 198: 440–445

Leichnetz GR, Spencer RF, Smith DJ (1984) Cortical projections to nuclei adjacent to the oculomotor complex in the medial dien-mesencephalic tegmentum in the monkey. J Comp Neurol 228: 359–387

Lestienne F, Vidal PP, Berthoz A (1984) Gaze changing behavior in head restrained monkey. Exp Brain Res 53: 349–356

Libet B, Gleason CA, Wright EW, Pearl DK (1983) Time of conscious intention to act in relation to onset of cerebral activity (readiness-potential). Brain 106: 623–642

Mountcastle VB, Lynch JC, Georgopoulos A, Sakata H, Acuna C (1975) Posterior parietal association cortex of the monkey:

command functions for the operations within extrapersonal space. J Neurophysiol 38: 871–908

Orgogozo JM, Larsen B (1979) Activation of the supplementary motor area during voluntary movements in man suggests it works as a supramotor area. Science 206: 847–850

Rubens (1975) Aphasia with infarction in the territory of the anterior cerebral artery. Cortex 11: 239–250

Schlag J, Schlag-Rey M (1970) Induction of oculomotor responses by electrical stimulation of the prefrontal cortex of the cat. Brain Res 22: 1–13

Woolsey CN, Settlage PH, Meyer DR, Spencer W, Hamuy TP, Travis AM (1952) Patterns of localization in the precentral and "supplementary" motor area and their relation to the concept of a premotor area. Res Publ Assoc Res Nerv Ment Dis 30: 238–264

Received November 10, 1984 / Accepted December 18, 1984