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Ear and eye representation in the frontal cortex, area 8b, of the macaque monkey: an electrophysiological study

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Abstract We evoked both ear and eye movements in area 8b, the rostral area of frontal cortex, in two monkeys. In some sites it was possible to evoke only ear movements or only eye movements; in other locations we evoked both ear and eye movements by varying the intensity of electrical stimulation. The electrically evoked ear movements were forward, or backward, or oblique (upward-forward; upward-backward). In two penetrations the ear movements were bilateral, in the other penetrations they were contralateral. Ipsilateral ear movements were not observed. The evoked eye movements were mainly fixed-vector saccades, contralateral and with an upward orientation of about 45°. If we considered only the sites where the threshold was equal to or lower than 50 μA, the stimulation of this area evoked mainly ear movements. In addition we recorded the electrical activity of 195 neurons. Of these neurons: 74% (145/195) discharged before ear movements (ear cells); 20% (40/195) discharged before ear and eye movements (ear-eye cells); 5% (10/195) discharged only before eye movements (eye cells). Ninety-one percent (132/145) of ear cells presented a preferred direction; 90% (36/40) of ear-eye cells presented a preferred direction for ear movements, and 15% (6/40) presented a preferred direction for eye movements. Eighty-five percent (34/40) of cells did not present a preferred direction for visually guided saccades and were active when the monkey made saccades toward the unlit targets (checking saccades). Our results show that a field of area 8b is related to ear movements and to eye-ear movements. The findings that it is possible to obtain both ear and eye movements with low-intensity currents and that there are cells firing for the two types of movements suggest that area 8b may be involved in the orientation and coordination of both ear and eye. This area might be considered a rostral extension of supplementary eye field (SEF) or a different region. However, based on its distinct functional characteristics and connectivity, it is probably better regarded as a separate field. Regardless, the combination of 8b and SEF may constitute a cortical center for orienting processes.

Key words Frontal cortex · area 8b
Eye and ear movements · Orienting · Unit activity
Monkey

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Introduction

The dorsomedial frontal cortex of macaque monkey is made up of superior area 6 (Brodmann 1905) and area 8b of Walker (1940). The anterior part of superior area 6 is also named area 6aβ (Vogt and Vogt 1919) or FC and part of FB (Von Bonin and Bailey 1947). Mott and Schaefer (1890) found that electrical stimulation of area 6aβ evoked eye movements in the contralateral direction. Later Levinsohn (1909) also electrically evoked eye movements caudally (area 6aβ) and ear movements rostrally (area 8b).

The involvement of area 6aβ in oculomotor processes has been investigated, and a region where neurons are related to spontaneous and visual guided saccades has been found by Schlag and Schlag-Rey (1987); they called this area the supplementary eye field (SEF). Moreover, fixation cells were described (Bon and Lucchetti 1990, 1992; Schlag et al. 1992). In addition, Schall (1991) described many types of sensory and motor cells. He suggested a sensorimotor integrative role for SEF in skeletal and oculomotor movements. SEF has been reinvestigated by Russo and Bruce (1993) to verify whether eye movements are organized in craniotopic or retinotopic coordinates.

During a previous study, in agreement with Levinsohn (1909) and Schlag and Schlag-Rey (1987), we noted that electrical stimulation rostrally to SEF evoked ear movements. Furthermore, Parthasarathy et al. (1992) noted again the presence of electrically evoked ear movements in and around SEF in the monkey.

The aim of this report was to elucidate the characteristics of both ear and eye movements evoked by stimulation and the information encoded by unit activity of area 8b. Preliminary results were presented at the 23rd Annual Meeting of the Society for Neuroscience, Washington D.C., 1993.

Materials and methods

Behavior

The experiments were carried out on two *Macaca fascicularis*. The animals were cared for in accordance with European Community standards for the care of laboratory animals. They were trained on fixation and saccade tasks. Preliminary training was done with the apparatus mounted on the monkey's home cage. Each monkey learned to press a bar to illuminate a bicolored, light-emitting red/green diode (LED; Siemens LS110). After a random time period (0.5–5.0 s), the LED turned from red to green for a fixed period of time (0.5 s). The animal had to release the bar during the green period to receive a liquid reward. After the monkey learned to perform this fixation task in the cage, it was taught to sit in a primate chair and perform a saccade task. In this task several LEDs could become red before the last one turned green. Each LED switched on simultaneously with the offset of the previous LED. The animal had to release the bar during the green period to receive a liquid reward. An acoustic cue marked the start of the task; the animal was then free to begin the trials at will. The acoustic cue remained on throughout the series of trials and switched off at the end. The LEDs, which were 0.05° in diameter, were positioned 200 cm in front of the monkey.

The trial was not aborted if the animal made an extra saccade. During the task the animal sometimes made extra saccades to the unlit targets, apparently to check whether the LED was on. We considered these extra saccades self-initiated, probably because the monkey disliked losing the reward, and we called them "checking saccades."

After the monkeys learned to perform the saccade task, they were prepared for the eye position measurement and head restraint. After 1 week the monkeys were trained with the head fixed in place until they performed the saccade task successfully at a level of 90–100%. Then the animals were prepared for the recording of unit activity.

We tried unsuccessfully to train one monkey to move the ear in selected directions. In order to obtain ear movements in all possible directions, we oriented the ear with scratches or noises. When we stopped the acoustic stimulation, the monkeys moved the auricle and we recorded these self-initiated ear movements. With this approach, generally the movements of both ears were symmetrical.

In order to verify whether one or both ears were involved in the unit activity, we tried to test only one ear, but this approach was unsuccessful, since the animal generally moved both ears. Owing to the difficulty of this approach, we abandoned the attempt to observe the ear movements as social signals, which are significant in nature. During these experiments we kept the two animals alert by delivering some drops of water between tasks.

Surgery

Using aseptic techniques, with the monkeys under general anesthesia (ketamine 10 mg/kg i.m. and intravenous thiopental sodium), one hollow stainless steel cylinder was attached to the skull with four screws and cemented in place to allow a painless fixation of the head. A search coil was implanted subconjunctivally (Judge et al. 1980), and four stainless steel wires were inserted into the neck muscles to monitor the electromyographic activity (EMG). Then, a stainless steel chamber for the electrophysiological investigation was implanted vertically in each hemisphere.

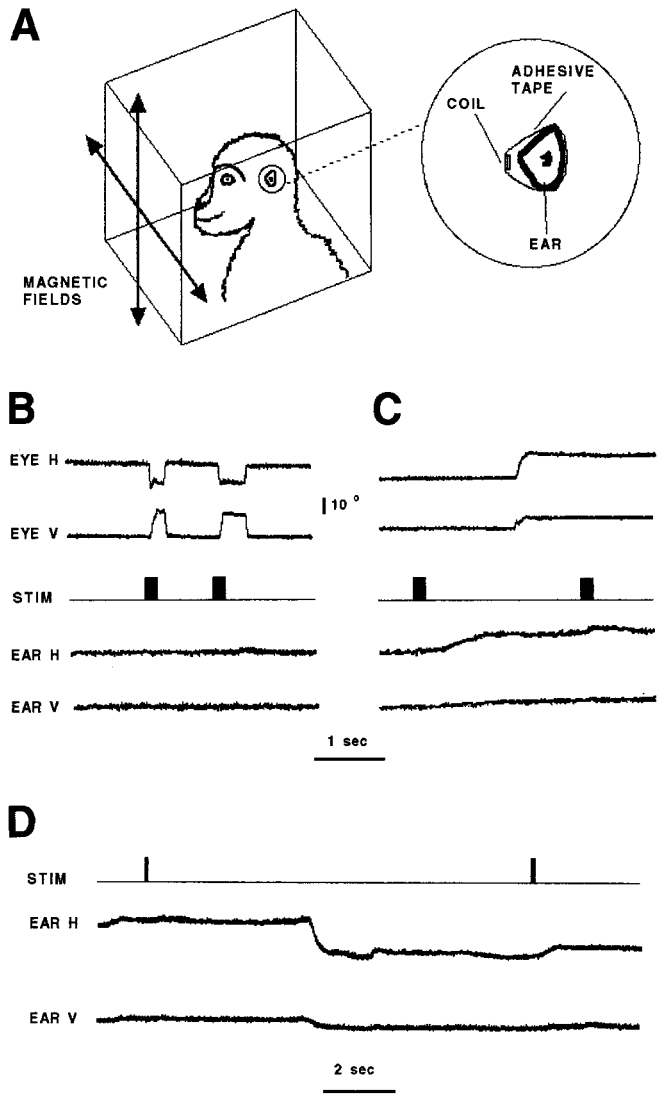


Fig. 1 **A** Method of recording ear movements. The coil was attached to the auricle by adhesive tape at each experimental session. The same magnetic fields allow both ear and eye movement recordings. **B** Evoked saccades; **C** evoked ear movements. **D** Example of stimulation with the ear in different positions: the first stimulation is ineffective; the second stimulation, with the ear in a different position, is effective (position dependent). Ear and eye signals have a different gain. (*EYE H, V* horizontal and vertical components of eye movements, *STIM* electrical stimulus, *EAR H, V* horizontal and vertical components of ear (auricle) movements)

Physiological methods and data analysis

Eye movements were recorded by the search coil technique, using the phase-detection method (Remmel 1984). The same technique was used for ear movements, applying a search coil to the ears of each animal with adhesive tape at the start of each experimental session (Fig. 1A). This system allowed us to define the beginning and end of an ear movement, but not other parameters (Fig. 1B,C). In fact, our search coil system defines a movement in two dimensions (x-y) while the ear movements are in three dimensions (x-y-z). At the same time we used a TV infrared system and videotape to observe the movement on- and off-line. The camera was positioned as the experimental situation required.

With this approach we were able to record a signal with x and y coordinates. We could then define the timing of the ear move-

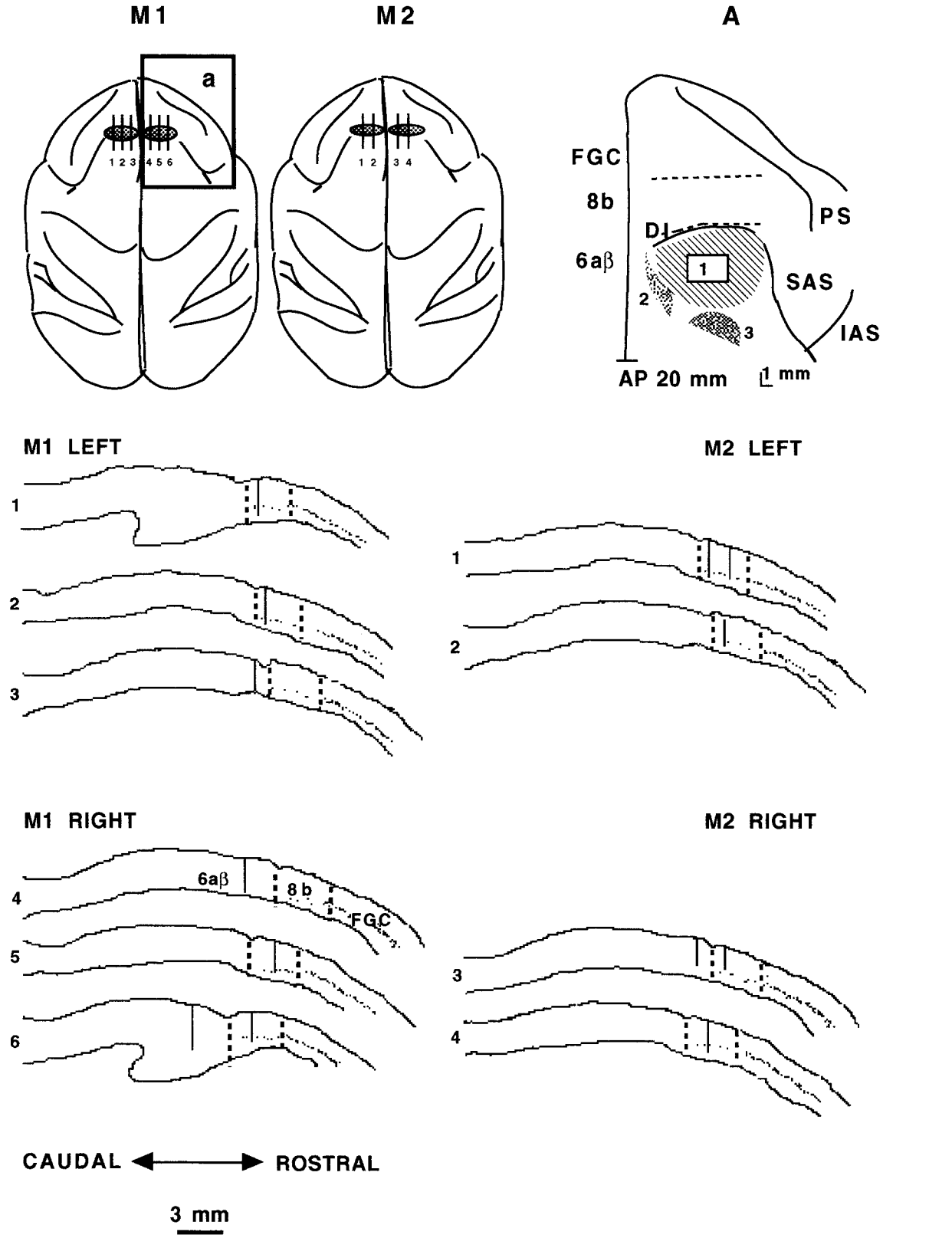


Fig. 2 *Top*: view of brains of two monkeys (*M1*, *M2*), the *small dark ellipses* indicate the zones of investigation. *A*, Magnification of one of four studied regions (*a*). *FGC* frontal granular cortex, *8b* disgranular cortex, *6aβ* agranular cortex; *1-2-3* investigated zones caudal to 8b: *1* cortical zone with cells related to eye (SEF), eyebrow, eyelid, mouth, neck, trunk, and shoulder movement, *2* cortical zone with prevalently arm-cells, *3* cortical zone with leg and hip joint-cells; *PS* principal sulcus, *SAS* superior arcuate sulcus, *IAS* inferior arcuate sulcus, *DI* dimple from a blood vessel. *Bottom*: Sections of four hemispheres where coagulation marks (*vertical lines*) were made. The *dashed lines* show the borders of cortical area 8b with area 6aβ and frontal granular cortex (*FGC*); *marks* represent the granular cell layer

ment with the unit discharge and compare the x- and y-signal with that observed by both experimenters on- and off-line with the infrared TV system. When the evoked movement or the unit activity were ambiguous, we observed the ear movement directly and rejected doubtful results of stimulation or unit activity. Electrical stimulation was induced using a two-channel stimulator connected to two constant-current stimulus isolation units, wired to provide biphasic square-wave pulses. The stimulation was executed every 500 μ in each penetration by epoxylite-coated tungsten electrodes, while the monkeys were alert and looking around in a brightly lit or dark room, or during attentive fixation task.

The ear movements were evoked with an intensity of current ranging from 20 to 85 μA, a frequency of 250 Hz, and a duration ranging from 70 to 120 ms. The eye movements were evoked with an intensity of current ranging from 15 to 100 μA, a frequency of 330 Hz, and a duration ranging from 70 to 120 ms. We used two different frequencies of stimulation since we observed that one was best to move the ear and one, the eye.

The evoked eye and ear movements were distinguished from self- generated movements, using the following criteria: (1) the movement had to follow at least 60% of threshold stimulations; (2) the starting position had to be the same for the eye and approximately the same for the ear auricle; (3) the delay had to be constant ($\pm$20 ms).

The EMG activity of the neck muscles monitored the animal's attempts to rotate the head. Single neurons were isolated with epoxylite-coated tungsten electrodes that were advanced through the dura with a hydraulic microdrive (Narishige MO-95B). The microelectrode signal was amplified (Bak MDA-4) and passed through a custom-built band-pass filter (500–7500 Hz) to eliminate artifact from the 50- and 75-kHz coil drivers. Then it passed through a window discriminator (Wpi 121) that generated unit pulses to be sampled by the computer. The eye and ear movements, stimulus, and spike activity were sampled at 1 kHz and stored by a Macintosh system for off-line analysis.

Coagulation marks were made by d.c. (10 μA for 15 s) at some of the recording sites, for histological reconstruction. At the end of the experiments, the animals, under deep anesthesia, were perfused with a 0.9% NaCl solution followed by 5% formalin. Subsequently, the brain was sectioned in 60-μm slices and stained with thionin.

Results

We studied area 8b with electrical stimulation and unit activity recording. The cytoarchitectonic organization indicated that stimulation and recording sites were localized in the frontal disgranular cortex, area 8b of Walker (1940), and in the anterior frontal agranular cortex, area 6aβ (Fig. 2). In these experiments we localized in area 6aβ many different type of cells: (1) saccade and fixation cells (SEF) together with cells related to ear, mouth, neck, trunk, and shoulder movements (Fig. 2A, 1); and (2) a region with mainly arm cells medially (Fig. 2A, 2) and some leg cells more caudally (Fig. 2A, 3). The neurons recorded in area 6aβ are under investigation; as a first approximation, we have recognized a rough somatotopic organization.

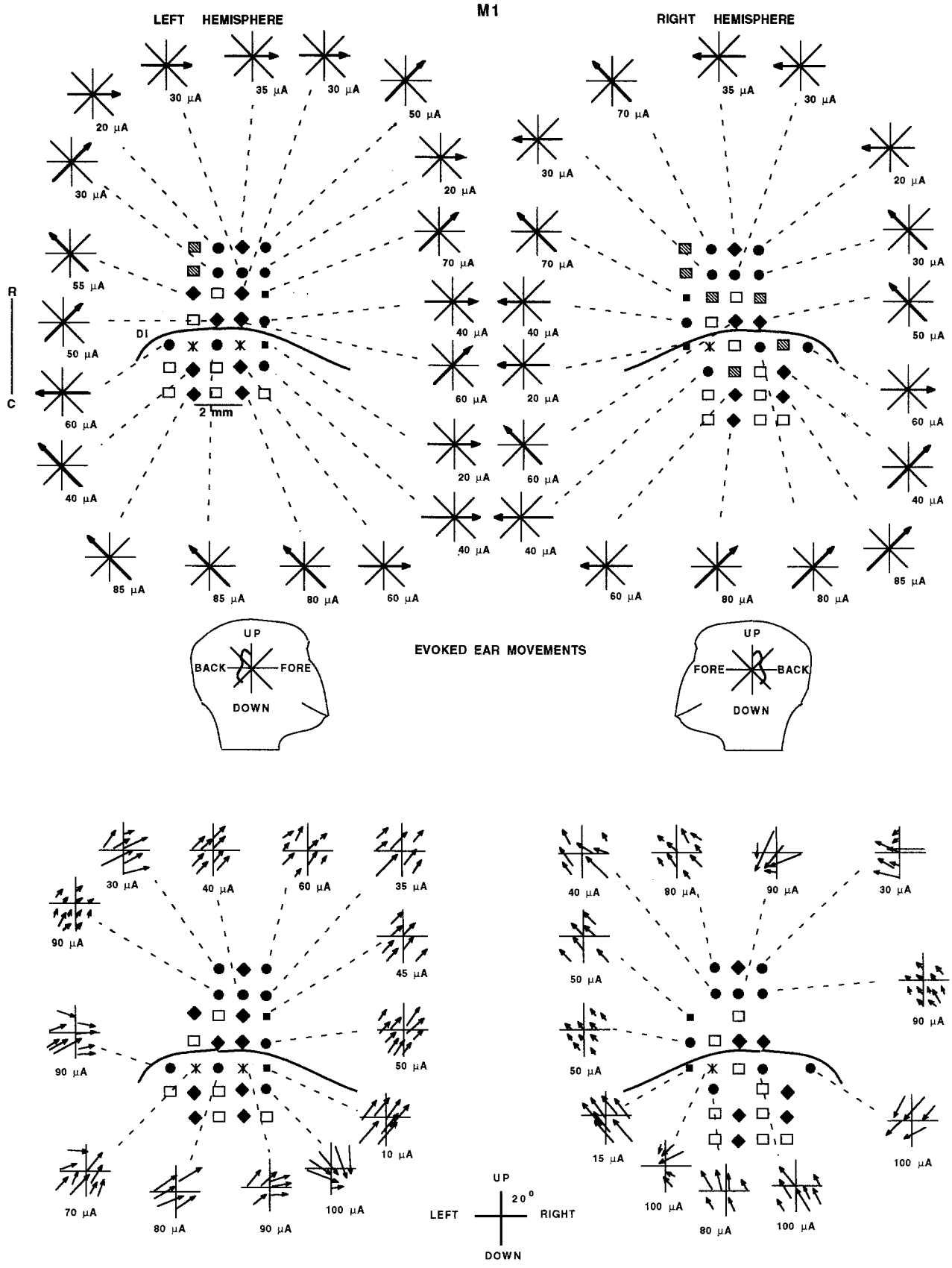
Stimulation study

In the two animals, in four hemispheres, we found locations in which it was possible to evoke only ear or only eye movements; in other locations we evoked both ear and eye movements varying the intensity of electrical stimulation (Figs. 3, 4). The electrical stimulation evoked the movement of both ears in only two penetrations; in the other cases the ear activated was contralateral. In some penetrations it was impossible to define the correct direction because of poor collaborative behavior of the animal.

In our experiments the evoked ear movements were strictly position dependent (Fig. 1C,D). If the monkey maintained the ear forward at the time of stimulation, we did not obtain a forward movement. In order to evoke an ear movement in a certain direction, we had to stimulate when the ear, moved by the animal, was still in a different spatial position. We defined the direction of movements during and after the experiment by reconstruction of single frames of videotape. The direction of movement was accepted when the two researchers agreed on it. The oblique directions were approximated to 45°; this value represents a mean of at least five stimulations for each site. Since the animal moved the auricle itself, it was difficult to stimulate repetitively with the auricle exactly at the same spatial position. Most of the electrically evoked ear movements observed in our experiments were forward, backward, and oblique (upward-forward, upward-backward). Even if a clear map does not exist, the forward and upward-forward movements were represented medially, while the backward and upward-backward movements were represented laterally (Figs. 3, 4).

The evoked eye movements were usually fixed-vector saccades, and only occasionally did we find end-directed saccades or mixed directions (Figs. 3, 4). For fixed-vector saccades, electrical stimulation was not effective at all when the animal was performing a fixation task, even if we increased the current intensity by twice or more. On the contrary, the electrical stimulation could elicit end-directed saccades during the fixation task; but the current had to be doubled and the eye movements were smaller than when the animal was not fixating. Most of the fixed-vector saccades were contralateral, with an orientation of about 45° upward, and the amplitudes of evoked saccades were mainly independent of the starting orbital position.

Fig. 3 Representation of the brain area of one monkey (M1) studied with electrical stimulation. The dimple (*DI*) is the landmark for the penetrations, which are oriented rostrocaudally *from top to bottom*: (*R* rostral, *C* caudal). *Top*: representation of evoked ear movements. *Arrows* represent the mean direction of ear movements in each site; current threshold values are shown. *Bottom*: representation of evoked eye movements. The *arrows* represent the directions at each site; current threshold values are shown. (*EAR* penetrations where electrical stimulation evoked only ear (auricle) movements, $EAR>>>EYE$ penetrations where the current threshold to evoke ear (auricle) movements was lower than that to evoke the eye movements, $EAR<<<EYE$ penetrations where the current threshold to evoke ear (auricle) movements was higher than that to evoke eye movements, *EYE* the penetrations where stimulation evoked only eye movements, *undefinable direction* in these sites we were unable to define the true direction of ear or eye because of poor collaborative behavior of the animal)


M1
LEFT HEMISPHERE
RIGHT HEMISPHERE
R
C
DI
2 mm
30 μA
35 μA
30 μA
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30 μA
20 μA
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UP
20°
LEFT
RIGHT
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EYE
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UNEXCITABLE SITE

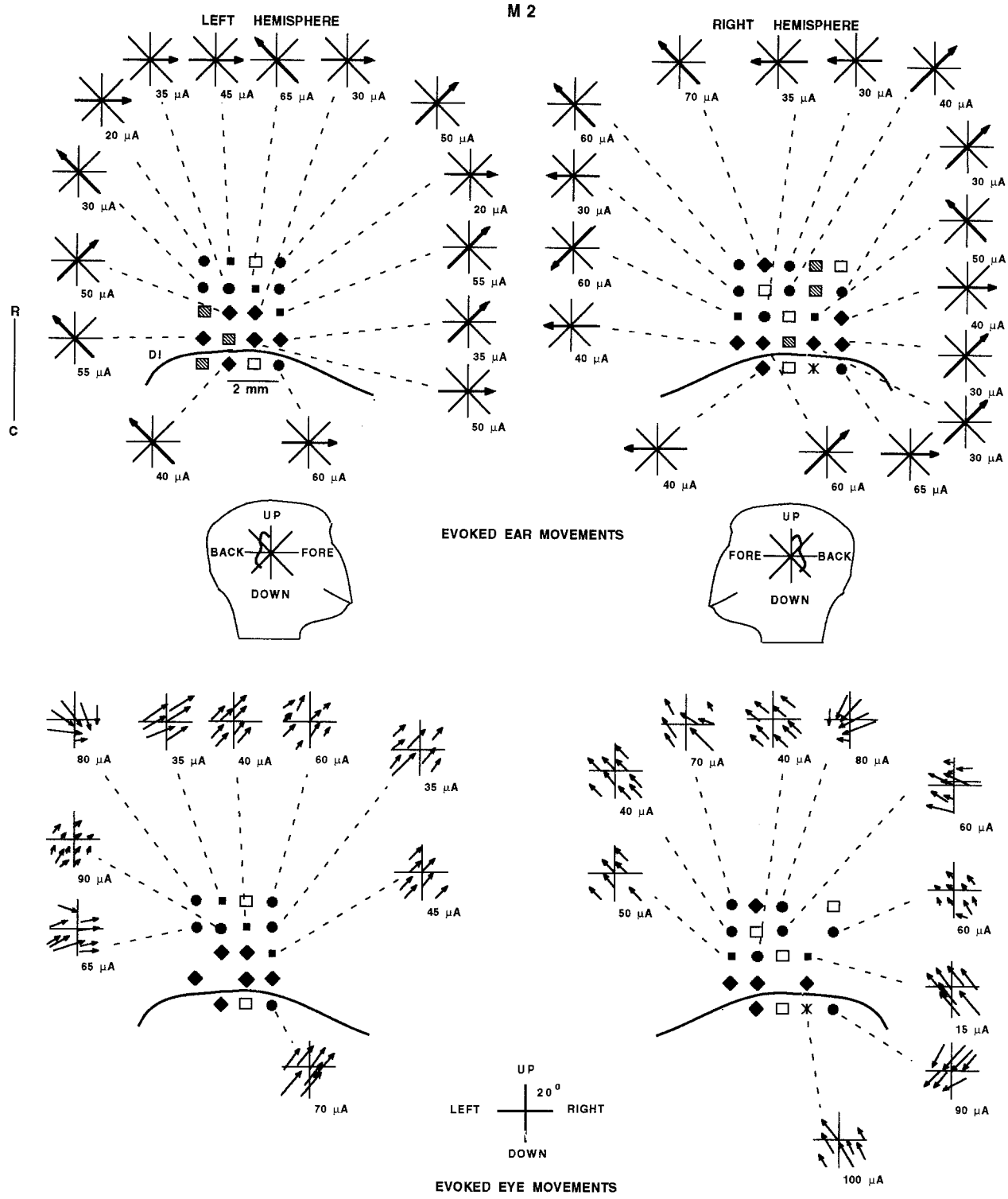


Fig. 4 Representation of the brain area of one monkey (M2) studied with electrical stimulation. The dimple (*DI*) is the landmark for the penetrations, which are oriented rostrocaudally, from *top to bottom* (*R* rostral, *C* caudal). *Top*: representation of evoked ear movements. *Arrows* represent the mean direction of ear movements in each site; current threshold values are shown. *Bottom*: representation of evoked eye movements. The *arrows* represent the directions at each site; current threshold values are shown. (*EAR* the penetrations where electrical stimulation evoked only ear (auricle) movements, *EAR>>>EYE* the penetrations where the current threshold to evoke ear (auricle) movements was lower than that to evoke the eye movements, *EAR<<<EYE* the penetrations where the current threshold to evoke ear (auricle) movements was higher than that to evoke eye movements, *EYE* the penetrations where stimulation evoked only eye movements)

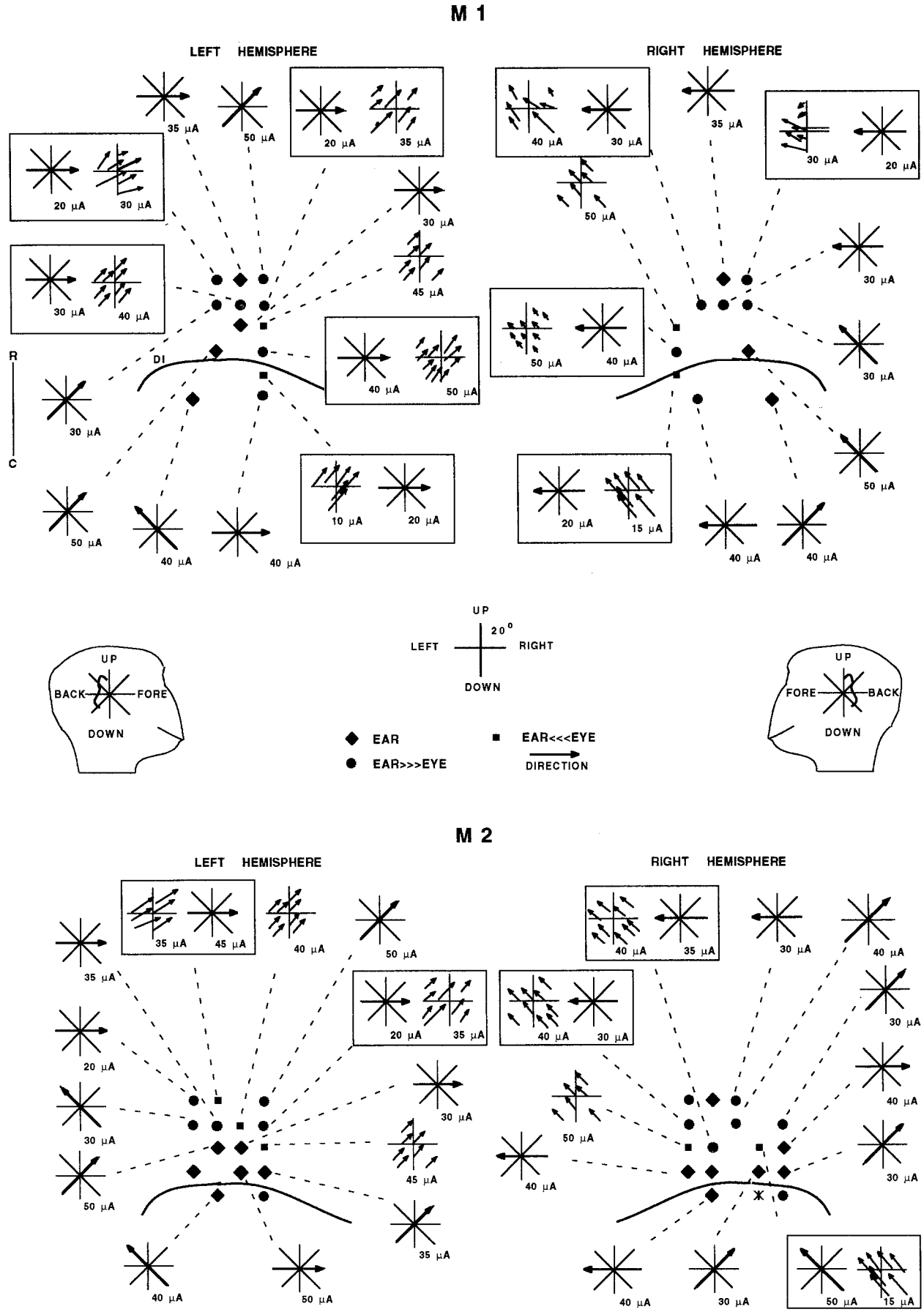


Fig. 5 Representation of ear, eye, and both ear and eye movements evoked with a current threshold equal to or less than 50 µA in monkeys M1 and M2

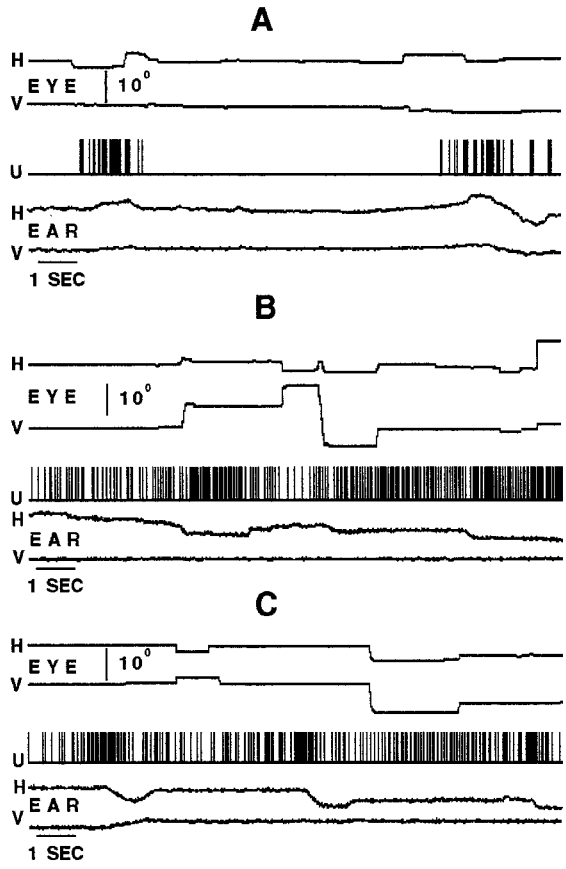


Fig. 6 Examples of unit activity recordings: **A** burst cells; **B** tonic activity; **C** burst-tonic activity. (*H* horizontal component, *V* vertical component, *U* unit activity)

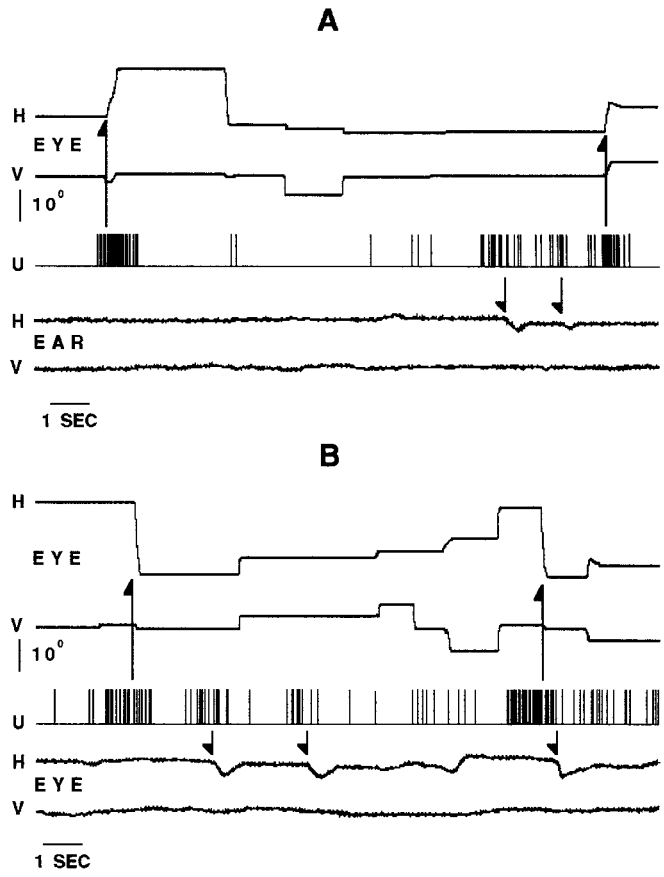


Fig. 7A,B Examples of ear-eye cells. These cells showed a burst of activity before both ear and eye movements, and also showed a preferred direction for both ear and eye movements

The electromyogram of neck muscle activity did not show increased activity during the stimulation phase. In each penetration, the threshold was higher in the superficial layers, and in most penetrations the direction of evoked movements, eye or ear, was the same at all levels of stimulation.

In accordance with Bruce and Goldberg (1985) we considered focal points of stimulation those in which low current intensity, equal or inferior to 50 μA, could elicit ear or eye movements. This approach emphasized that stimulation of area 8b evoked mainly ear movements, then ear-eye movements, and rarely pure eye movements. It is interesting to observe also that, in the sites where both ear and eye movements where evoked, the threshold for ear movements was often lower (Fig. 5).

In the focal points where we found ear-eye movements, the directions of ear movements were forward, and eye movements were contralateral and upward. In addition, we observed that when the animal performed an attentive fixation the threshold for evoked ear movements was unchanged. The delay of both ear and eye evoked movements ranged from 40 to 200 ms, most frequently from 50 to 150 ms.

Unit activity recording

We recorded the electrical activity of 301 neurons. One-hundred cells were discarded, as it was impossible to define with certainty the ear movement direction. The inability to define the ear direction was a consequence of poor collaborative behavior of the animals during some penetrations, particularly in the second monkey (M2). Of the remaining 201 cells, 6 of them were active for acoustic stimuli and were not related to ear or eye movements. Of 195 neurons 74% (145/195) discharged before ear movements, 20% (40/195) discharged before ear and eye movements, and 5% (10/195) discharged only before eye movements.

The recorded ear cells showed the following patterns of activity: burst, tonic, and burst-tonic (Fig. 6). The ear-eye cells discharged before both ear and eye movements with a double burst of activity (Fig. 7) and tended to be located where the electrical stimulation evoked ear-eye movements with low current intensity. The lead time of the discharge ranged from 200 to 1400 ms for ear movements and from 400 to 1400 ms for eye movements. More frequently the lead time for both ear and eye movements was from 600 to 900 ms. The onset of discharge was selected when the interspike interval was

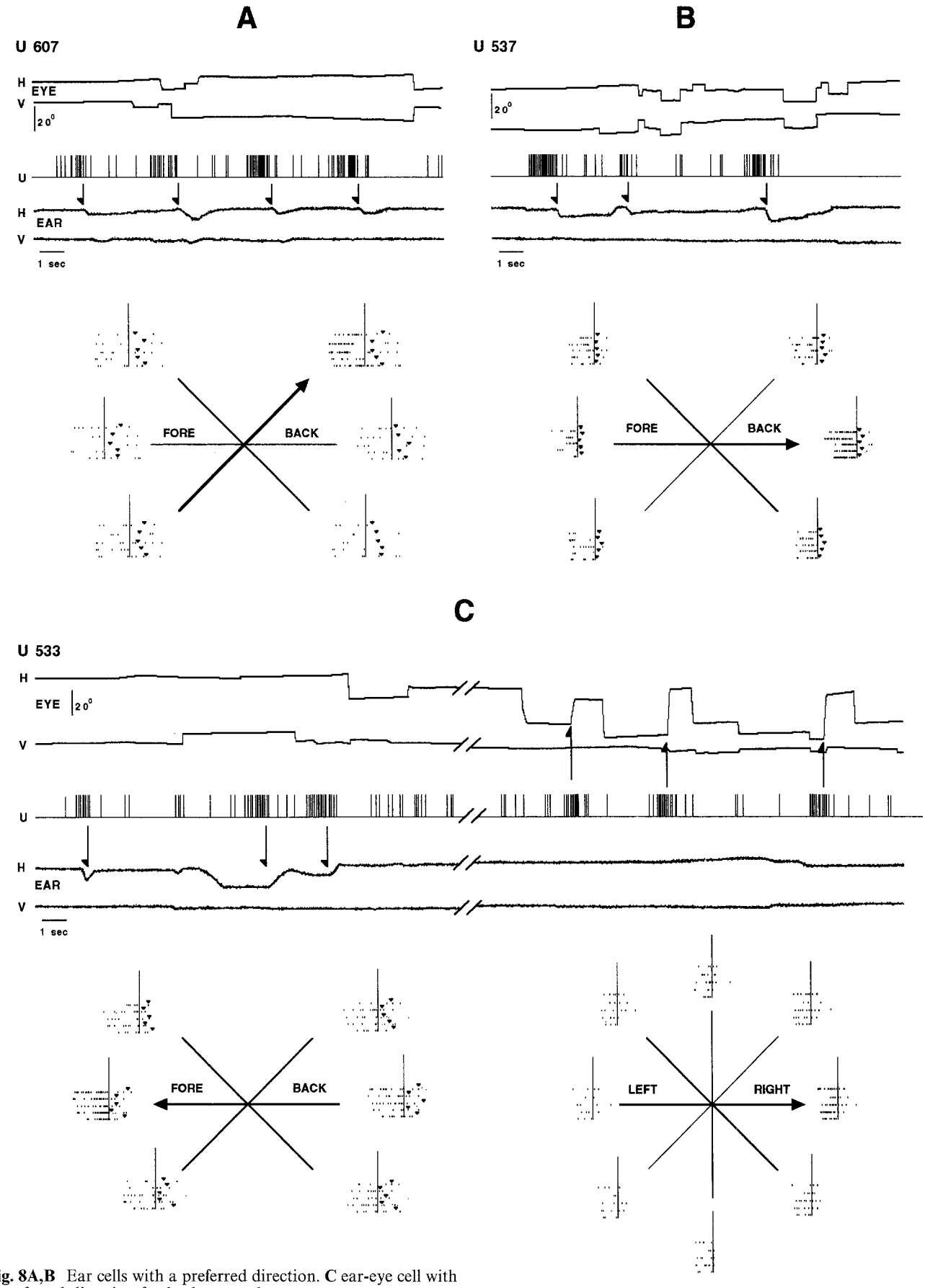
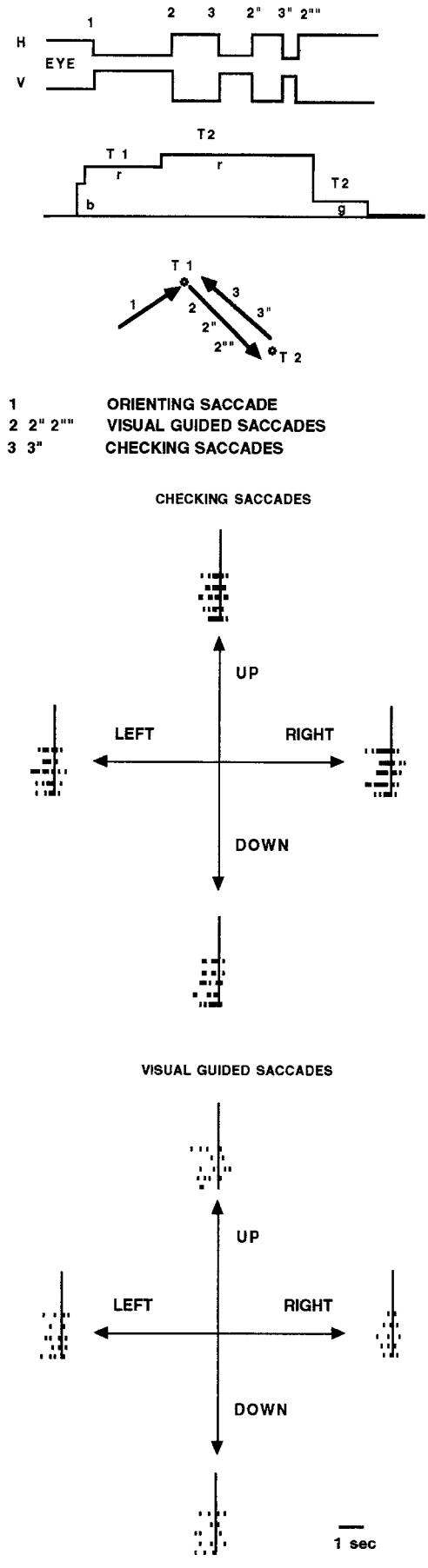


Fig. 8A,B Ear cells with a preferred direction. **C** ear-eye cell with a preferred direction for both ear and eye movements



equal to or less than 100 ms. This value was arbitrarily selected in relation to spontaneous and evoked movement activity frequency, as reported below.

A preferred direction was observed in 91% (132/145) of ear cells, with a mean discharge frequency of 18 spikes/s (SD $\pm$ 5 sp/s). The spontaneous activity of these cells was very low (2 $\pm$ 2 sp/s; Fig. 8A,B). Of the other cells (13/145), 6 neurons did not show a clear selectivity for direction, but discharged in all directions tested, 7 cells discharged for position (4 tonic neurons) and for position and direction (3 burst-tonic neurons).

The animals did not move the ear along the vertical axis spontaneously or in response to electrical stimulation. A preferred direction was observed for ear movement in 85% (34/40) of ear-eye cells and 15% (6/40) presented preferred direction for eye movements (Fig. 8C). The mean discharge frequency for ear movements was 18 sp/s (SD $\pm$ 5 sp/s). The activity for eye movements was 21 sp/s (SD $\pm$ 3 sp/s). Spontaneous activity was very low (2 $\pm$ 2 sp/s).

The 6 neurons with a selective direction were active for visually guided saccades. The other 34 neurons discharged when the monkey made an extra saccade toward unlit targets. We considered such extra saccades as self-initiated, probably because the monkey disliked losing the reward, and called them checking saccades. These checking saccades did not show a selective direction (Fig. 9).

During the recordings the ear cells showed a preferred direction in many penetrations similar to that evoked by the electrical stimulations. Moreover, the cells recorded in the same site of penetration could present different preferred directions. This aspect might be related to the angle of the electrode with the surface of the cortex. The maps (Fig. 10) illustrate the direction encoded by the majority of cells or those found in the superficial layers. Although it should be noted that these results were obtained from only two monkeys and from a small sample of cells, a clear distribution of directions does not appear; however, the forward movements seem to be represented medially and backward movements, laterally.

Fig. 9 *Top*: saccade task and saccade behavior. After the animal pressed the bar (*b*), the first target (T1) turned red (*r*); when T1 turned off, the second target (T2) turned red, then green (*g*), and during this period the animal released the bar to receive the reward. Saccade *2* was the first saccade toward T2, while saccade *3* was a "checking" saccade toward T1, which was unlit. The trial was not aborted if the animal moved the eye away from the correct target. (*2", 2""* visually guided saccades, *3"* checking saccade). *Bottom*: Cells showed brisk activity during checking saccades and weak or background activity during visually guided saccades. These ear-eye cells did not show a preferred direction for eye movement

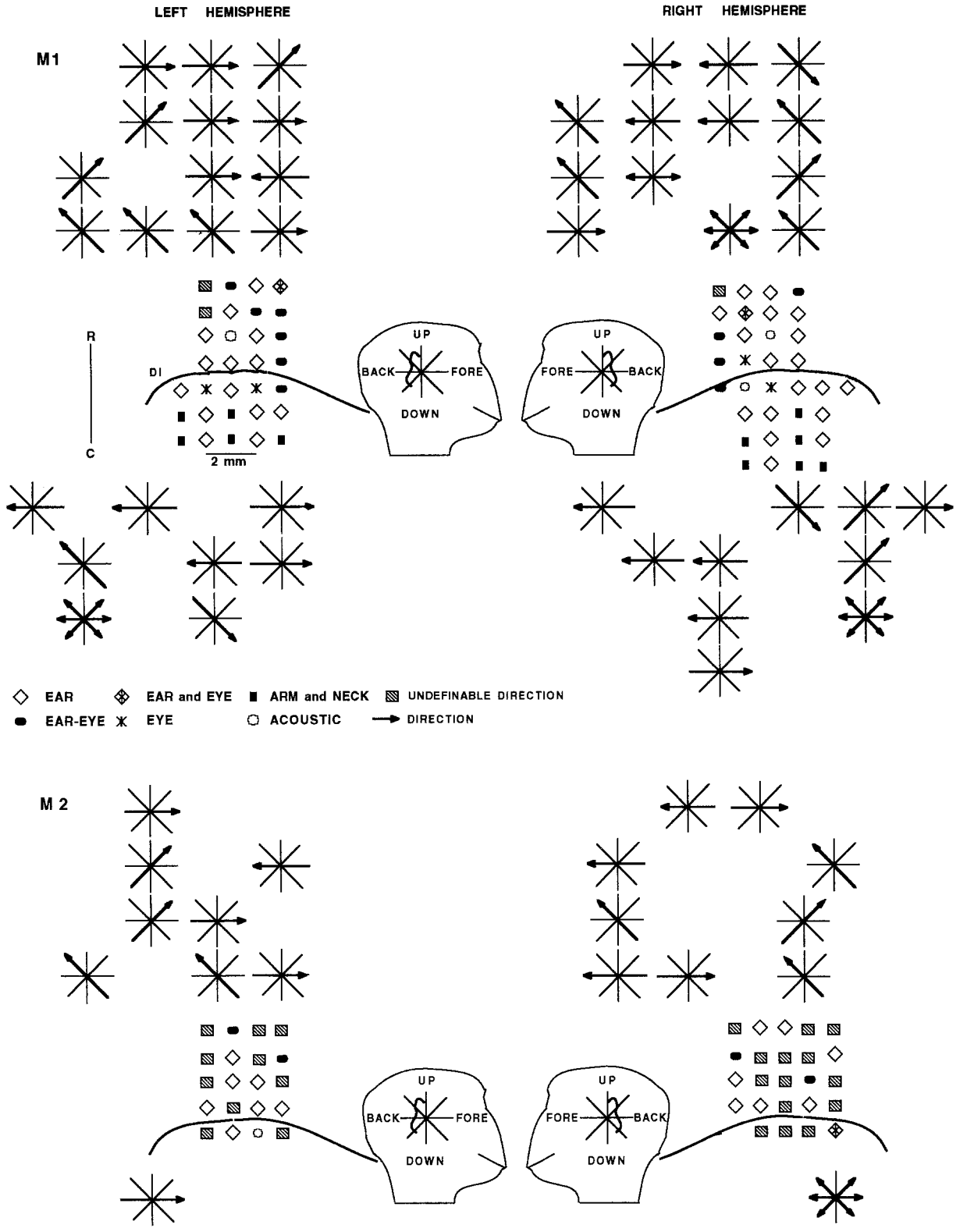


Fig. 10 Map of ear directions coded by ear and ear-eye cells in monkeys M1 and M2. In four penetrations the cells did not show a preferred direction. In three penetrations we found both ear and eye cells. In M2 the representation of ear direction (undefinable direction) is scarcer than in M1 because of poor collaborative behavior of M2

Discussion

The present study demonstrates that stimulation evokes mainly ear movements and ear-eye movements in area 8b, with a preferred direction and with a threshold equal or less than 50 μA. The evoked saccades are mainly of the fixed-vector type, and attentive fixation inhibits eye but not ear movements.

These data are in apparent disagreement with those of Mitz and Godschalk (1989). They evoked mainly goal-directed eye movements in area 8b. These differences could be the consequence of many factors: (1) the difficulty in evoking ear movements (position dependent); (2) the different frequency of electrical stimulation used to evoke eye and ear movements; (3) different primate species and behavioral conditions; (4) different sites that show diverse evoked patterns.

In our study the recording of electric activity of single cells showed discharge neurons related to a preferred direction of ear movements. In most ear-eye cells the direction selectivity affected only ear movements. The cells are characterized by a long lead time with a peak value of 1400 ms and a mean value of 800 ms for both ear and eye movements. Similar long-lead burst neurons were described by Tanji et al. (1980) in supplementary motor cortex. The authors suggested that the differences in the delays in motor areas might be related to the rank of the motor area. Particularly, motor areas with a consistent number of long-lead bursters are involved in the initiation of movement and intentional processes.

The presence of ear-eye cells with eye activity unrelated to parametric characteristics of checking saccades suggests the presence of an activation phenomenon. These cells are characterized by a complex dichotomous behavior: (1) they are specific for direction of ear movements; (2) they are unspecific for the direction of eye movements, but specific for self-initiation of eye movements without a trigger signal.

Other investigators have noted evoked ear movements in different areas of prefrontal and frontal cortex related to eye movements in frontal eye field (FEF; Russo and Bruce 1993) and in SEF (Schlag and Schlag-Rey 1987; Partasarathy et al. 1992). The inconsistent reports about ear representation in these areas could be related to the difficulty in evoking ear movements. Alternatively, SEF and FEF might be more involved in eye control than in ear and eye control.

The presence of ear-eye cells suggests further considerations. Animals in nature move the ear auricle to improve localization of noises in the environment. Humans have lost this behavioral ability, but have kept the eye-head coordination. At present, we have more knowledge about eye-head movement coordination and the neural structures involved (Hyde and Toczek 1962; Bizzi et al. 1971; Roucoux et al. 1980; Zangermaister and Stark 1982; Van der Steen et al. 1986; Peck 1990). than about ear-eye coordination. If we extend the possible duality of mechanisms found for eye-head coordination to ear-eye coordination, we might consider this field as a center for ear-eye coordination.

The open question is: should this field be considered an extension of SEF or a different area? Previous reports localized SEF in the agranular frontal cortex caudal to area 8b. The principal differences between SEF and this zone are: (1) during recording activity and stimulation we did not find cells related to arm movements or visual cells, both of which have been found in SEF area 6aβ (Schlag and Schlag-Rey 1987; Bon and Lucchetti 1992; Schall 1991); (2) few sites of stimulation evoked end- or goal-directed saccades, and most evoked saccades were certainly fixed vector; (3) sites with double evoked movements have not been described in SEF; (4) the threshold was higher for ear movements caudally to area 8b. In addition, preliminary anatomical results regarding the connections of area 8b and area 6aβ suggest that different projections do exist. Particularly, area 8b is connected with 6aβ and not with FEF, while SEF is strictly connected with FEF (Camarda et al. 1991). A cortical zone specific for ear movements was found by Burman et al. (1988) near the FEF.

Conclusions

The presence of very long lead bursters in relation to self- initiated ear and eye movements suggest that this field in area 8b is involved in the initiation of these two movements, and it may be considered a high-rank center involved in premotor activity, particularly to localize sounds in space. The cytoarchitecture of area 8b and the physiological and preliminary anatomical results suggest that this field is not SEF proper, but the cortical connections hint that it is closely linked with SEF. We propose that this zone is a premotor center for ear-eye coordination for orienting processes. In addition, the observations that: (1) the localization of this cortical zone near SEF related to ear movements; (2) there is a similar zone near FEF; (3) there are strict connections between SEF and FEF; and (4) FEF is involved in aurally guided saccades (Russo and Bruce 1994) suggest that areas FEF and SEF, with their neighboring ear zones, might be involved in parallel and serial controls of spatial localization of sounds.

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