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GENERATION OF RAPID EYE MOVEMENTS IN 3 DIMENSIONS

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ABSTRACT

The anatomy, physiology, and pathophysiology of rapid eye movement generation was investigated in the rhesus monkey. The brainstem reticular formation was systematically explored with single neuron recordings, electrical stimulation, and chemical inactivation. The riMLF was identified as the area that generates vertical and torsional rapid eye movements in parallel to the PPRF for horizontal movements.

The vestibulo-ocular reflex compensates for head movements about any axis in 3-dimensions space, but the gain for torsional movements (rotation about the naso-occipital axis) is smaller than for horizontal or vertical movements. Visually induced saccades or pursuit movements, however, move the eyes with only two degrees of freedom as described by Listing's law (2, 5, 7, 15). We investigated brainstem areas associated with rapid eye movement generation and asked to what extent neurons code eye movements in 2 or in 3 dimensions.

Methods

Juvenile rhesus monkeys were chronically prepared with a head holder, a stereotaxically placed receptacle for a micromanipulator over a trephine hole, and a dual search coil to monitor eye positions (9). Single neuron activity was recorded with tungsten microelectrodes. Animals were placed onto a 3-dimensional vestibular turntable totally enclosed by an optokinetic sphere. In addition, small lights fixed to the sphere could be used as fixation stimuli.

Analysis

After careful calibration (10), search coil data were converted to rotation vectors of eye position (4).

Behavioral Data

Fig. 1A shows eye positions during torsional nystagmus, Fig. 1B eye positions in the same animal during spontaneous eye movements in the light. The oculomotor range of torsional eye movements during nystagmus is about +/− 15 deg, and thus is considerably smaller than the range in the horizontal (+/− 40 deg) or in the vertical (+/− 30 deg) direction. In a similar way, gain is smaller in the torsional direction, adding to the asymmetry in the output of the vestibulo-oculomotor reflex. However, when the animal makes spontaneous eye movements with the head upright and stationary, there are no systematic torsional movement components. The same applies to smooth pursuit movements. We tested more paradigms, all with the same result that visual input, if not a full-field optokinetic one, produces eye movements which are restricted to 2 dimensions.

Superior Colliculus

Neurons in the deeper layers of the superior colliculus are active prior and during saccades. Their causal role in the generation of saccades is based on the close temporal relation between neuron activity and eye movements, the fact that electrical stimulation elicits saccades, and the

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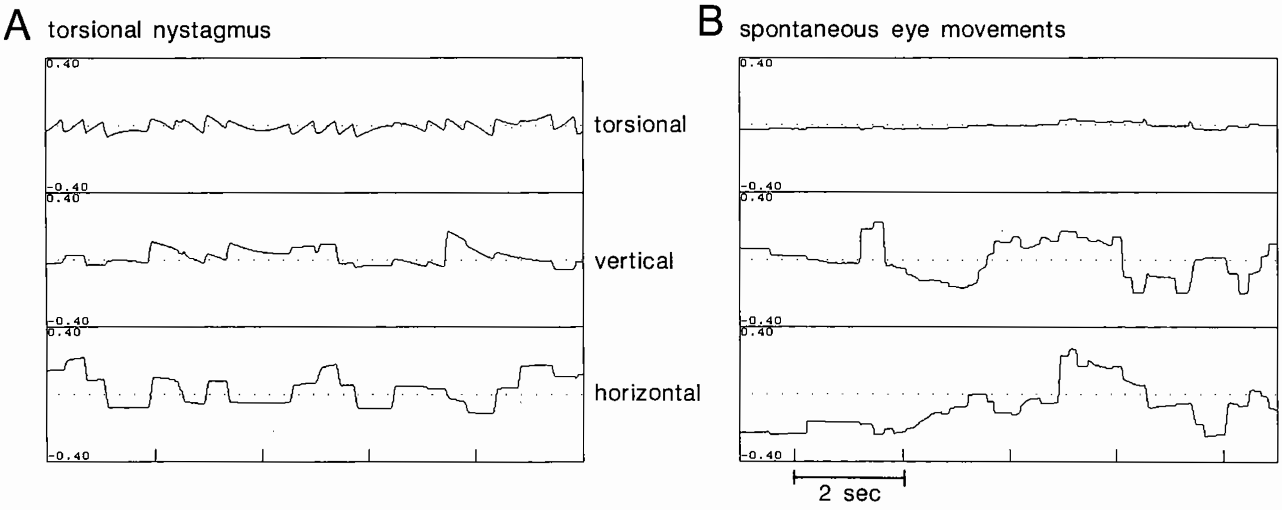

Fig. 1 A: Eye positions over 10 s of torsional nystagmus, and B: During spontaneous eye movements in the light. From above, the torsional, vertical, and horizontal trace. Note in B the contrast between the negligible torsional, but large excursions in the vertical and horizontal directions. The dotted line indicates primary position, position range +/− 40 deg.

projection to oculomotor areas in the brainstem which contain burst neurons (review: ref. 12). Single unit recordings in the deeper layers consistently revealed that neurons code eye positions in only two dimensions. Correspondingly, electrical microstimulation generated eye displacements with a fixed horizontal and vertical component (16).

Rostral Interstitial Nucleus of the Medial Longitudinal Fasciculus (riMLF)

An anatomical definition of this area has been given by Büttner-Ennever (1). It contains short-lead burst neurons projecting to vertical and oblique motoneurons (11). Our analysis showed that neurons display on-directions in a continuous way between pure vertical and pure torsional. Whereas neurons with up or down on-directions lie intermingled, they are segregated according to their torsional component of on-direction (17). Neurons displaying a positive torsional component (extorsion of the right eye) are all found on the right side of the brainstem, whereas neurons with a negative torsional direction component are on the left side. Electrical microstimulation on the right side leads to conjugate torsional movements in a positive direction. Inactivation of neuron populations leads to a deficit with loss of all torsional movements in one direction only, while vertical eye movements are slowed. Only if the riMLF is inactivated bilaterally, a loss of all rapid eye movements with a vertical or torsional component is found.

Motoneurons

With the monkey in an upright position and the head not moving, motoneuron behavior can be described 2-dimensionally in terms of iso-frequency curves (8). We now extended these investigations by recording motoneurons while the monkey had been put in different static roll positions. This adds a varying amount of torsion, *i.e.* counterrolling, while visually elicited eye movements still obey Listing's law (3). Data points can be approximated by a second-order surface giving the relation between activity in a motoneuron and all possible eye positions (14).

CONCLUSIONS

The vestibular system detects angular and linear acceleration in 3 dimensions and elicits compensatory eye movements also in 3 dimensions. Whereas the labyrinth seems to detect angular accelerations in an isotropic way, vestibulo-ocular reflexes show clear directional asymmetries (6). The retina is a 2-dimensional structure and projects to topographically arranged maps with different magnification factors in the cortex and superior colliculus. We could show that the superior colliculus as one of the interfaces to the oculomotor system is also organized in a 2-dimensional way. Only the riMLF together with the PPRF, the immediate premotor structures to generate rapid eye movements, code movements in 3 dimensions. It remains unclear how the same neuron populations generate eye movements in 3 dimensions within the context of vestibular input, and generate eye movements in 2 dimensions obeying Listing's law with visual input. It has been suggested that this reduction of degrees of freedom in the motor space greatly simplifies not only central computation, but also interaction of various sensory inputs, as well as coordination of motor output, like eye-head, or gaze-arm coordination (13). Although eye movement generation shows many specializations as compared to the general motor system, we think that organizational principles like reduction of degrees of freedom applies to all motor systems.

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