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ANTICOMPENSATORY FAST PHASES OF THE VESTIBULO–OCULAR REFLEX IN CATS.

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Introduction

The anticompensatory fast phases (AFPs) of the vestibulo–ocular reflex (VOR) are important during both active and passive head movements to reset the eye to the center of the orbit and to direct the eye towards visual target during active head movements (1).

In previouds studies (2,3,4) plane–related differences in the amplitude of the AFPs have been shown in cats and rabbits. In fact, in frontally eyed animals, the AFPs of the vertical vestibulo–ocular reflex (VVOR) are much smaller than those of the horizontal VOR (HVOR) and in the laterally eyed animals the VVOR is characterized by the complete absence of AFPs (2).

In this study we attempted to analyze in cats the plane differences of the AFPs in the VOR. The amplitudes and frequencies of the AFPs were studied during stimulation at increasing velocities. We also compared the trajectories and final points of the AFP during horizontal and vertical vestibular stimulation at different head tilts.

Methods

Vestibular stimulation. The cats were placed in a cradle with their heads positioned at the center of rotation of a triaxial servocontrolled round table (3M–3000, Mangoni; Livorno, Italy). The table was oscillated with step waveforms at various velocities. Stimuli were delivered in yaw (HVOR), and pitch /VVOR) axes. Table movements were measured with a servo–potentiometer.

Detection of eye movements. Under topical anaesthesia a tiny suction cup bearing a light emitting diode (LED) was attached to the cat's eye. The LED projected a narrow beam of infrared light onto a photosensitive position detector (SC–50, UDT, Hawthorne, U.S.A.) 5 mm from the tip of the LED. The detector provided continuous X–Y indication of the position of the beam's incident centroid. It was found to be linear to within 5% for eye movements of ±15° and have a sensitivity of 0.2 min of arc. Before each experimental session the photosensor was positioned in such a way that the primary position of the eye corresponded to the zero of the detector.

Ocular torsion was also measured by positioning a second LED orthogonally with respect to the major axis of the suction cup to project the light beam onto a smaller X–Y photosensor (SC25 UDT) placed with its sensitive surface in the frontal plane to detect possible ocular torsion (5).

Results

1) Effect of stimulus velocity on the amplitude and frequency of anticompensatory fast phases (AFPs) in the horizontal and vertical planes. In the horizontal and vertical planes the compensatory eye responses to vestibular step stimulation were interrupted by anticompensatory fast phases (AFPs). In the horizontal plane the AFP cumulative amplitude increased linearly with stimulus velocity ($r = 0.98$, $m = 0.48$) (Fig. 1) This was caused by an increase of AFP mean amplitude ($r = 0.98$, $m = 0.27$) while the AFP frequency remained unchanged. Since the cumulative amplitude of the compensatory slow phases did not significantly change, the final eye position became more and more anticompensatory by increasing the stimulus velocity.

In the vertical plane the AFPs were 50–60 % smaller than those observed in the horizontal plane. By increasing stimulus velocity only a slight increase of AFP cumulative amplitude was found ($r = 0.89$, $m = 0.14$). This effect resulted only from increasing AFP frequency ($r = 0.93$, $m = 0.03$) because the AFP mean maplitude was almost unchanged ($r = 0.07$, $m = -0.002$) (Fig. 1).

2) Trajectory and final points of the AFPs. The AFP trajectories depended on the stimulation plane. Most of the AFP trajectories of HVOR were lying in the horizontal plane (Fig. 2) ($r = -0,94$; $m = 0.23$). The AFP trajectories of the VVOR showed a more spread distribution with respect to the HVOR, maintaining a slight preponderance of horizontal trajectories ($r = -0.75$, $m = -0.11$) (Fig.2).

As a consequence of the planar differences in trajectories, the final point positions showed a welldefined distribution with respect to the orbital coordinates (Fig. 3). The anticompensatory fast phases of the HVOR and VVOR ended into an elliptic area with the major axis oriented in the horizontal orbital plane. The ratio of the major axis of the ellipse to the minor one was 2–2.5.

By superimposing the final point distribution on the retina (Fig. 4), the distribution area corresponded to that of retinal ganglion cell zone with a density greater than 500 ganglion cells per mm^2.

3) AFP final point distribution at various head tilts. When the animal head was tilted from 0° to 30° in the frontal plane, no change of the AFP final point distribution with respect to the space was observed. Beyond this limit the major axis of this elliptic distribution tended to reduce more and more its alignment to the horizon until its inclination reached 30° – 45° at 90° side–down (Fig. 3). The tonic torsional eye reflex was also measured by tilting the animal at various degrees in the frontal plane. The increase of the head inclination caused a progressive reduction of the gain of the ocular responses. In particular the gain dropped down after 20°–30° of tilt (Fig. 5).

Discussion

The results of this study show that there are substantial differences in AFPs of HVOR and VVOR. In fact the AFP cumulative amplitude of HVOR increased by increasing the stimulus velocity. This effect was due to the increase of AFP amplitude rather than to the increase of AFP frequency.

Conversely, the mean amplitude of the AFPs in VVOR was smaller than observed in HVOR and tended to increase slightly by increasing the stimulus velocity. This effect was due to the increase of AFP frequency rather than to the increase of AFP amplitude.

We suggest that the AFP plane differences might be related to the shape of the maximum receptor density region of the retina (6). Because the horizontal axis of this zone is longer than its vertical axis, horizontal AFPs can displace the eye within a much wider spatial range. In fact, as stimulation velocity increases, the AFPs of the HVOR can increase in amplitude preventing a loss of the space continuity (Fig. 6). Maintenance of this continuity in the vertical

plane requires smaller anticompensatory movements to keep the image within the area of maximum receptor density. Therefore, during extensive vertical movement of the head, fixation of a distant visual target and image stability can be assured only by an increase of the fequency of the AFPs.

The trajectories of the AFPs of the horizontal and vertical VOR were also different. Those of the HVOR were characterized by a clear horizontal prevelance, whereas those generated by the VVOR were markedly inclined, instead to be vertical. It would seem that while the eye tends to assume a well defined position along the vertical meridian, the position it assumes along the horizontal meridian is much less defined. Our analysis of the end points of the AFPs confirms this finding: the positions at which the AFPs terminate are more widely distributed within the horizontal as opposed to the vertical axis.

In addition, if the orientation of the head was changed, major axis of the AFP final point distribution remained fixed in space, indicating that the system generating AFPs is influenced by otolithic information. The reorientation of the AFPs allows a maintenance of the AFP end points in the horizontal line within 30° of head tilt. Since the visual streak is kept almost in horizontal position within 20°–30° of head tilt by torsional reflex, we conclude that the reorientation of the reflex rapid movements is function of the visual streak spatial position.

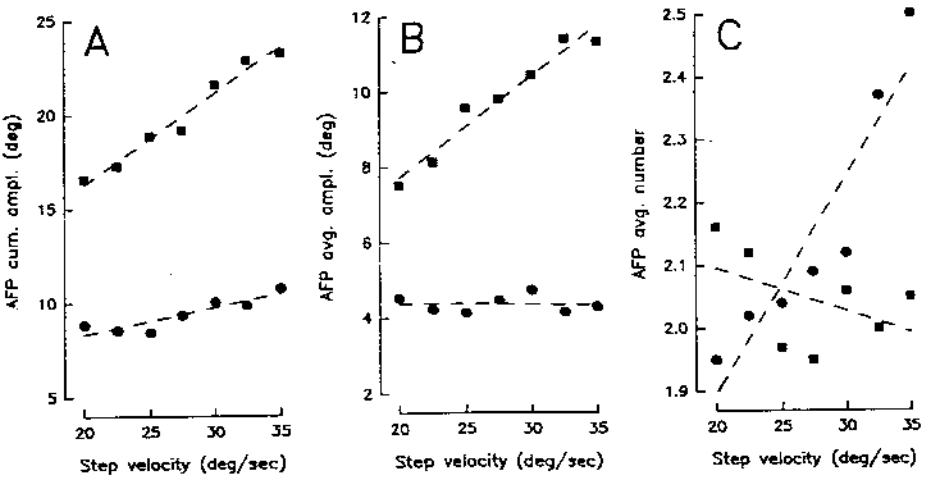

Figure 1: AFPs in response to various step velocities (amplitude: 20°) in the dark.
A:AFP cumulative amplitudes;
B:averaged amplitudes of AFPs;
C:averaged number of AFPs for each step.
Symbols: AFPs of HVOR (filled squares) and of VVOR (filled circles). Dashed lines: regression lines.

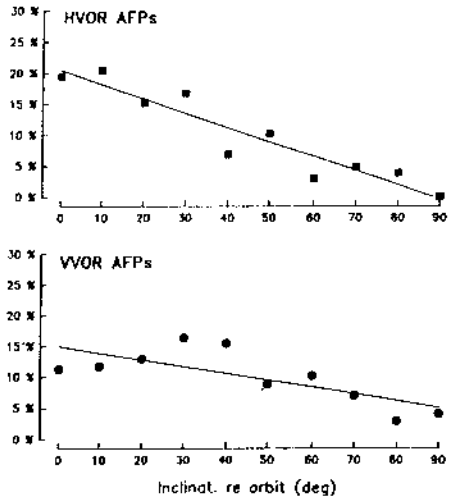

Figure 2: Percent distributions of AFP directions in the HVOR and VVOR. The 0 in the X axis indicates the horizontal orbital plane and 90 the vertical one. Each point represent percent distribution of directions within ±5°. Continuous lines: regression lines.

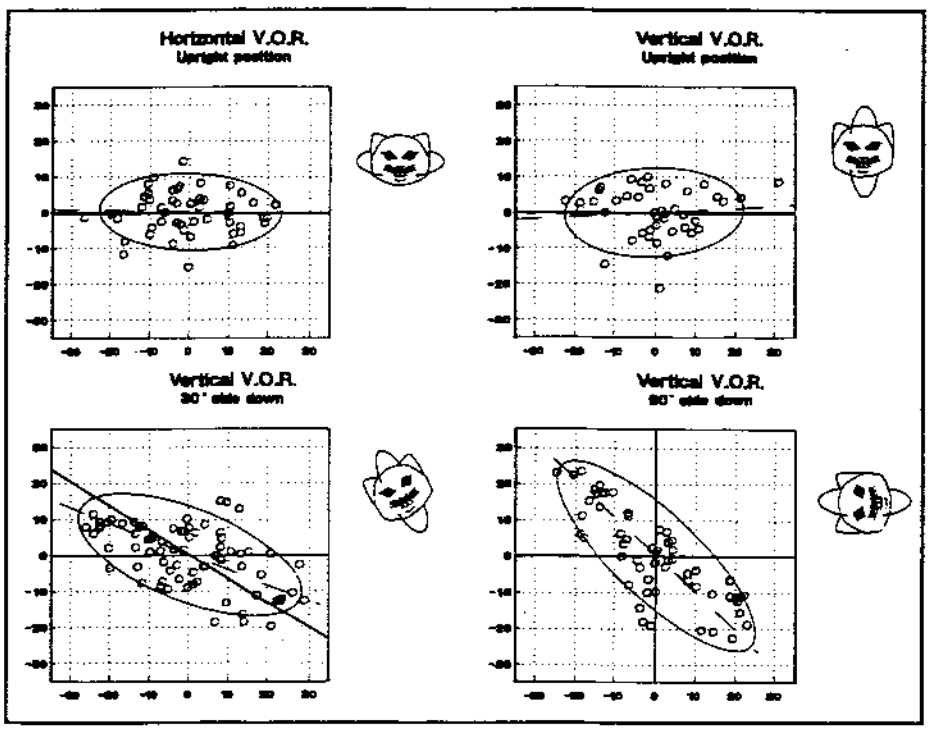

Figure 3: Influence of the head position on the final points of the AFPs in HVOR and VVOR at different animal positions (0° upright, 30° side down, 90° side down). The circles represent the final points in the orbital coordinate frames (expressed in degrees from the orbital center). Dashed line: regression line; continous lines: horizontal; ellipse diameters: ±2 SD.

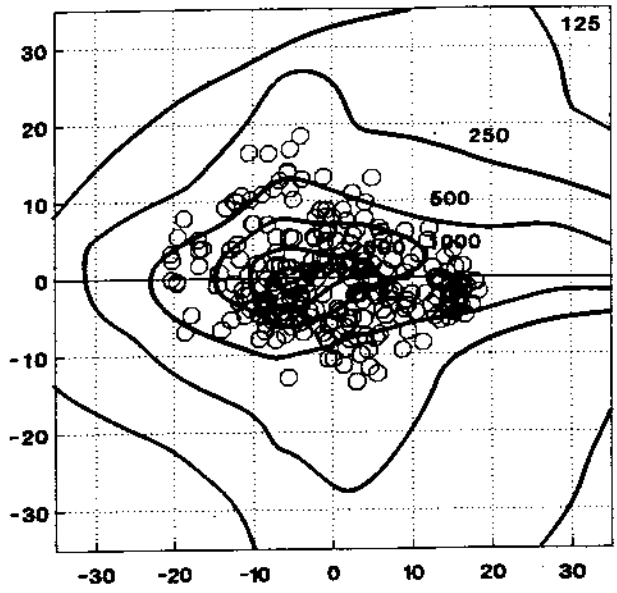

Figure 4: The final points of horizontal and vertical AFPs (circles) are superimposed on the retina. The ganglion cell isodensity lines are reported with their corresponding number of ganglion cells/mm^2.

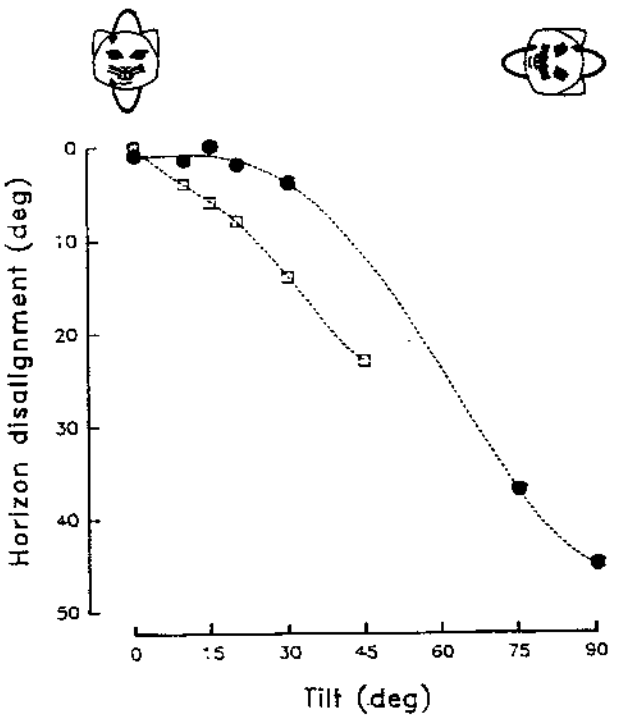

Figure 5: Disalignment of the horizon with the position of eye horizontal meridian (square) and major axis of AFP end point area (circle) at various head tilts.

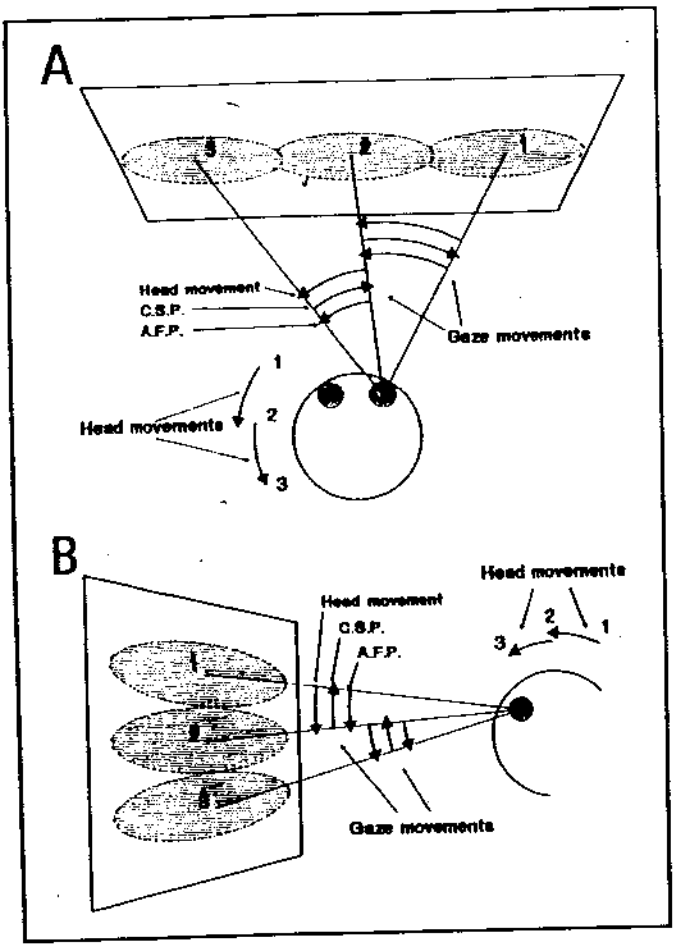

Figure 6: Schematic drawing of fast phase displacements during horizontal (A) and vertical (B) vestibular stimulations. The head displacement was subdivided in three different phases (1, 2, 3). The compensatory slow phases (CSP) and anti-compensatory fast phases (AFP) are reported in front of the head (arrows). It follows that the visual field was continuously explored by the high density receptor area of the retina (shadow area) through larger AFPs in the horizontal plane and small vertical ones in the vertical plane.

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