VOLUNTARY PRESETTING OF THE VESTIBULAR OCULAR REFLEX PERMITS GAZE STABILIZATION DESPITE PERTURBATION OF FAST HEAD MOVEMENTS

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SUMMARY

Normal subjects are able to change voluntarily and continuously their head-eye latency together with their compensatory eye movement gain. A continuous spectrum of intent-latency modes of the subject's coordinated gaze through verbal feedback could be demonstrated. It was also demonstrated that the intent to counteract any perturbation of head-eye movement, i.e., the mental set, permitted the subjects to manipulate consciously their vestibular ocular reflex (VOR) gain. From our data we infer that the VOR is always "on." It may be, however, variably suppressed by higher cortical control. With appropriate training, head-mounted displays should permit an easy VOR presetting that leads to image stabilization, perhaps together with a decrease of possible misjudgments.

INTRODUCTION

For some time it has been known that visual and mental effort influence the vestibular ocular reflex (VOR). Besides visual long- and short-term adaptation to reversing prisms (Melvill Jones and Gonshor, 1982) and fixation suppression of the VOR (Takemori and Cohen, 1974; Dichgans et al., 1978; Zangemeister and Hansen, 1986), the mental set of a subject can influence the VOR, e.g., through an imagined target (Barr et al., 1976; Melvill Jones et al., 1984) or anticipatory intent only (Zangemeister and Stark, 1981). In contrast to animals, human head and eye movements are governed by a conscious will of the human performer that includes verbal communication. Thus in a given experimental setup, the synkinesis of active human gaze may be changed according to instruction. The verbal feedback to the subject might permit a whole range of gaze types, even with amplitude and prediction of a visual target being constant. The gaze types (Zangemeister and Stark, 1982a) are defined by head minus eye latency differences (table 1). This has been demonstrated particularly by looking at the timing of the neck elektromyogram as the head movement control signal (Zangemeister et al., 1982b; Zangemeister and Stark, 1983; Stark et al., 1986). In this study, we compared the voluntarily changeable human gaze types performed during the same experiment with and without the addition of a randomly applied perturbation to the head-eye movement system. We tried to answer three questions in particular:

1. Are we able to modulate continuously the types of coordinated gaze through conscious intent during predictive active head movements?

2. What is the gaze (saccade and VOR/CEM (compensatory eye movement)) response to passive random head rotation from zero head velocity with respect to the preset intent of a given subject?

3. Does random perturbation of the head during the early phase of gaze acceleration generate responses that are the sum of responses to experiment (1) and (2)?

METHODS

Eye movements were recorded by monocular DC Electrooculography, head movements by using a horizontal angular accelerometer (Schaevitz) and a high-resolution ceramic potentiometer linked to the head through universal joints (Zangemeister and Stark, 1982c). Twelve normal subjects (age 22-25) attended a semicircular screen sitting in a darkened room. While they actively performed fast horizontal (saccadic) head rotations between two continuously lit targets at ±30° amplitude with a frequency around 0.3 Hz, they were instructed to focus on the following tasks: (1) "shift your eyes ahead of your head," (2) "shift your head ahead of your eyes." During (1) they were instructed to shift eyes "long before" (i, type II), or "shortly before" (ii, type I) the head. During (2) they were instructed to shift head "earlier" (i, type IIIA), or "much earlier" (II, type IIIB) than the eye, eventually "with the intent to suppress any eye movement" (type IIIB or IV). Each task included 50 to 100 head movements.

Perturbations were done pseudorandomly, (1) from a zero P,V,A (position, velocity, acceleration) initial condition of the head-eye movement system, and (2) during the early phase of head acceleration. They consisted of (1) fast passive head accelerations, of (2) short decelerating or accelerating impulses during the early phase of active head acceleration and were recorded by the head-mounted accelerometer. Perturbation impulses were generated through an apparatus that permitted manual acceleration or deceleration of the head through cords that were tangentially linked directly to the tightly set head helmet.

RESULTS

1. The subjects demonstrated their ability (fig. 1) to switch between gaze types in the experimentally set predictive situation of constant and large-amplitude targets. The respective gains (eye/head velocity) were: ty.II 0.9-1.1, ty.III 0.13, ty.IV 0.06-0.09. This result was expected from our earlier studies (Zangemeister and Huefner, 1984; Zangemeister and Stark, 1982a,c). The subjects showed differing amounts of success in performing the intended gaze type, with type IV being the most difficult to perform, supposedly because of the high concentration necessary (table 1).

2. Random perturbation of the head while in primary position, with head velocity and acceleration being zero (fig. 2), resulted in large saccades/quick phases of long duration, and a large and delayed VOR/CEM, if the subject had low preset intent to withstand the perturbation; in this case head acceleration showed a long-lasting damped oscillation. Respective gains were: figure 2 (upper): 0.35 (upper) 0.45 (lower); figure 2 (lower left): 0.5 (upper), 0.17 (lower). With increasing intent of the subject (fig. 2 left, middle, and lower), head acceleration finally became highly overdamped, but still with comparable initial acceleration values, and eye movements showed increasingly smaller and shorter quick phases as well as an early short VOR response. In addition, with the highest intent a late anticompensatory eye movement was obtained.

3a. Random perturbations of the accelerating head, i.e., sudden acceleration or deceleration of gaze in flight (fig. 3), were characterized by small VOR responses after the perturbation in case of high intent of the subject as in gaze type IIIB, or much higher VOR/CEM gain in case of low intent comparable to gaze type I. Respective gains were: figure 3 (left) ty.I 0.55, ty.3 0.06, ty.IV 0.08 (left), 0.09 (right); figure 3 (right): 0.13 (upper), 0.90 (lower).

3b. Random perturbations were also applied during coordinated head-eye movements in pursuit of a sinusoidally moving target (maximum velocity 50°/sec) with the VOR being suppressed through constant fixation of the pursuit target. Figure 4 (left) demonstrates the different amount of VOR fixation suppression as a function of changing intent during fixation of a sinusoidal target of the same frequency. With perturbation (fig. 4, right) a response was obtained that was comparable to the result of experiment (2). That is, depending on the subject's intent and concentration, the VOR response was low for high intent and vice versa (gain fig. 4, right: 0.044).

Therefore, the three initial questions could be answered as follows:

1. In nonrandom situations subjects can intentionally and continuously change their gaze types.

2. Gaze responses to passive random head accelerations depend on the subject's preset intent.

3. Perturbation of predictive gaze saccades in midflight results in the sum of tasks one and two.

DISCUSSION

The input-output characteristics of the VOR are subject to major moment-to-moment fluctuations depending on nonvisual factors, such as state of "arousal" (Melvill Jones and Sugie, 1972) and mental set (Collins, 1962). More recently, it has been found that the influence of "mental set" depends explicitly upon the subject's conscious choice of intended visual goal (Barr et al., 1976; Sharpe et al., 19081; Baloh et al., 1984; Fuller et al., 1983), i.e., following earth-fixed or head-fixed targets during head rotation. Consistent alteration of the mentally chosen goal can alone produce adaptive alteration of internal parameters controlling VOR gain (Berthoz and Melvill Jones, 1985). Obviously, comparison of afferent retinal slip detectors with concurrent vestibular afferents can be substituted by a "working" comparison made between the vestibular input and an efferent feedback copy of either the concurrent, or the imagined or anticipated concurrent, oculomotor output, as proposed by Miles and Eighmy (1980).

Our results here demonstrate the ability of the subjects to perform short-term adaptation during verbal feedback instructing for eye-head latency changes that changed the types of active gaze. These results are comparable to the data from Barr et al. (1976), in that an almost immediate change between different VOR gains with constant visual input could be generated. In addition, our perturbation experiments expanded these data, demonstrating the task- (or gaze-type) dependent attenuation of the VOR. This is in contrast to results in animals, where perturbation of

visually triggered eye-head saccades resulted in an acceleration of the eye (Guitton et al., 1984; Fuller et al., 1983), because a conscious task-influence of the VOR is impossible. Therefore not only can a representation of the target's percept (Barr et al., 1976) be created, but also an internal image of the anticipated VOR response in conjunction with the appropriate saccade.

We hypothesize that through the cortico-cerebellar loop a given subject is able to continuously eliminate the VOR response during predictive gaze movements. This is done internally by generating an image of the anticipated VOR response in conjunction with the appropriate saccade, and then subtracting it from the actual reflex response. This internal image can be manipulated intentionally and continuously WITHOUT a VOR on/off switch. In this way a flexible adaptation of the conscious subject to anticipated tasks is performed.

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Table 1.– Gaze types defined by latency: eye minus head latency. Type II: early prediction of eye, late head movement; eye movement dominates gaze. I: head follows eye shortly before eye has reached target; classical gaze type. III: head and eye movements start about simultaneously. Predictive gaze type. IV: early prediction of head, late eye saccade; head movement dominates gaze. Suppression of VOR/CEM in III and IV. See also figure 1b.

Type	Eyelatency-headlatency, msec	Average rate of success in generating intentionally different gaze types through verbal feedback,%
I	+50	76
II	<50	56
IIIa	>50-200	69
IIIb	>200-550	
IV	>550	16

II

HORIZONTAL CAL. 1 SEC
VERTICAL CAL. 10 DEG.
$ 10000 DEG/SECsq

(a)

EYE POSITION

III

HEAD ACCELERATION

IV

CONTINUOUS CHANGE OF GAZE TYPES WITH CHANGE OF INTENT
(CHANGING HEAD-EYE LATENCY)

50 DEG

0 DEG

BEGIN OF HEAD MOVEMENT

END OF HEAD MOVEMENT

0.2 SEC

HEAD POSITION

50 DEG

0 DEG

TYPE: II   I   III   IV

50 DEG

0 DEG

-50 DEG **(b)**
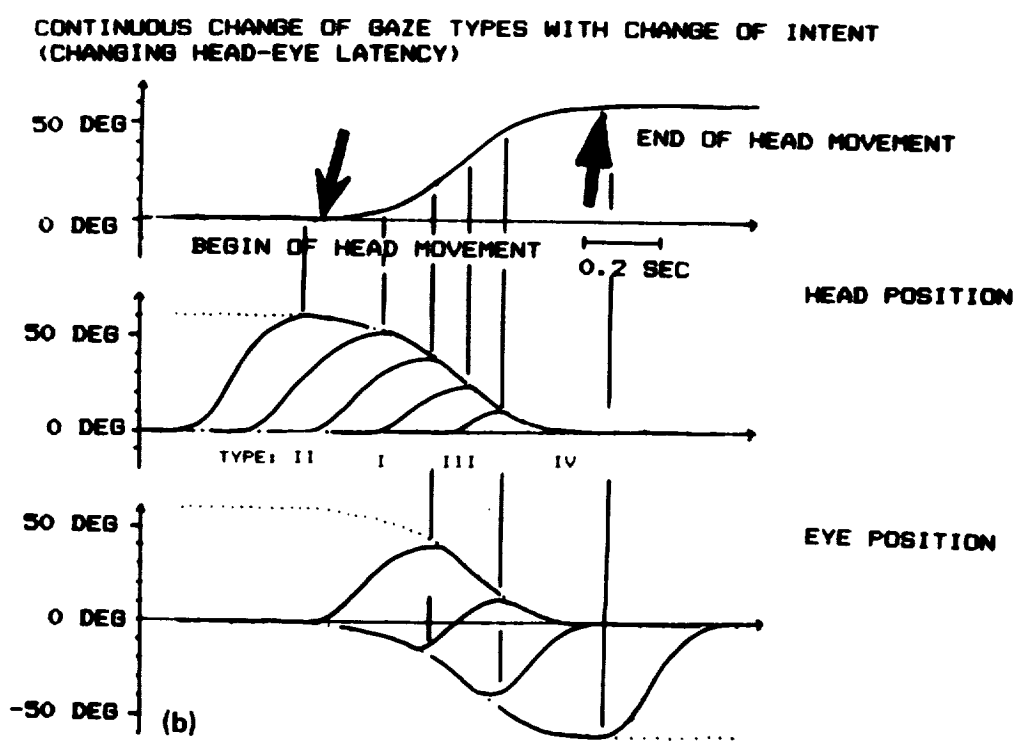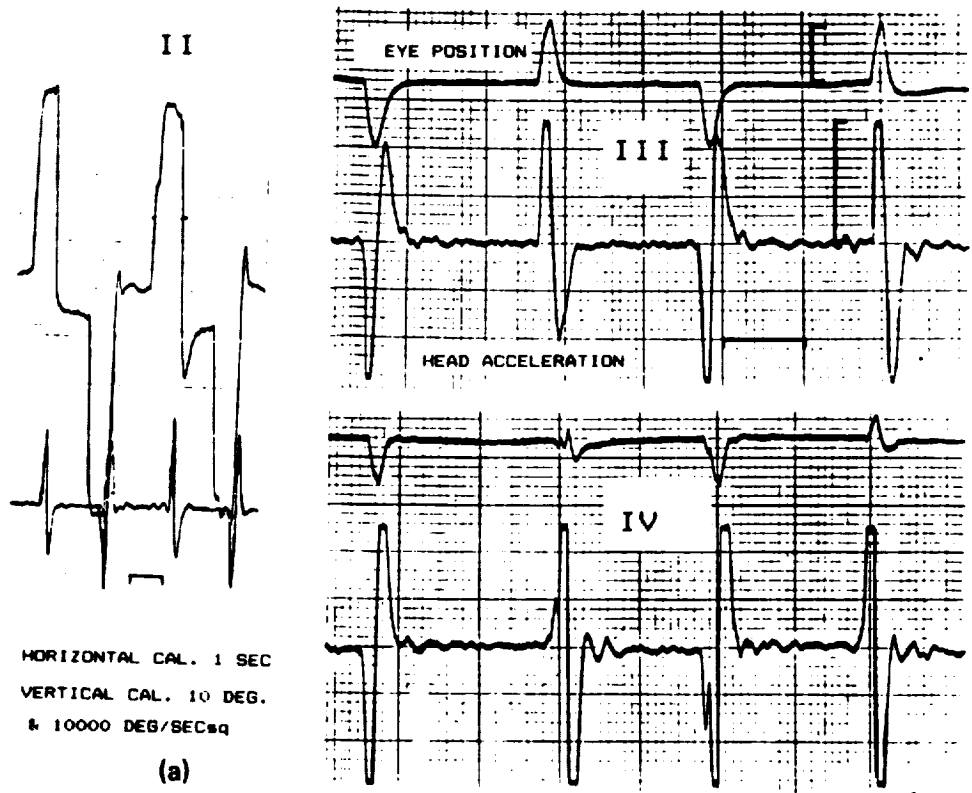
EYE POSITION

Figure 1.– a) Gaze types 2, 3, 4 generated intentionally through verbal feedback (upper).
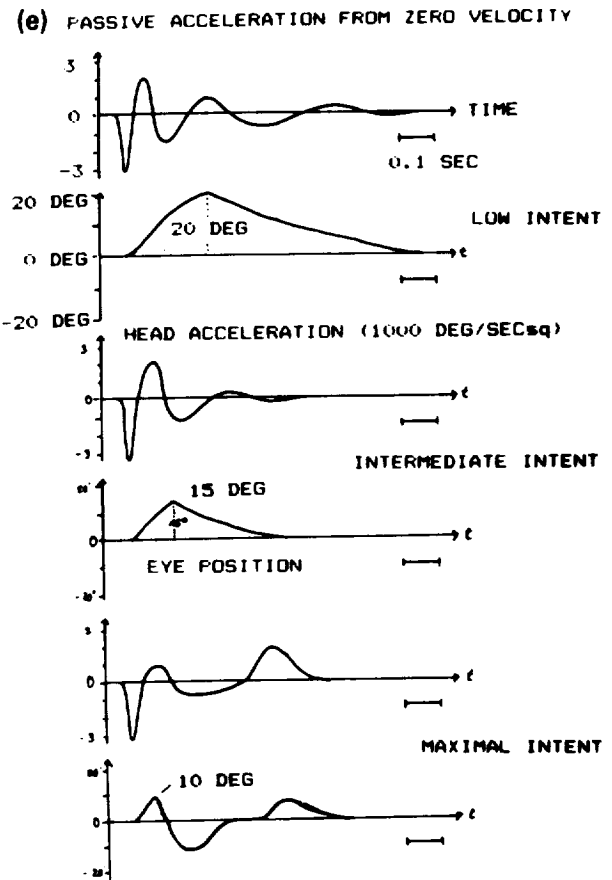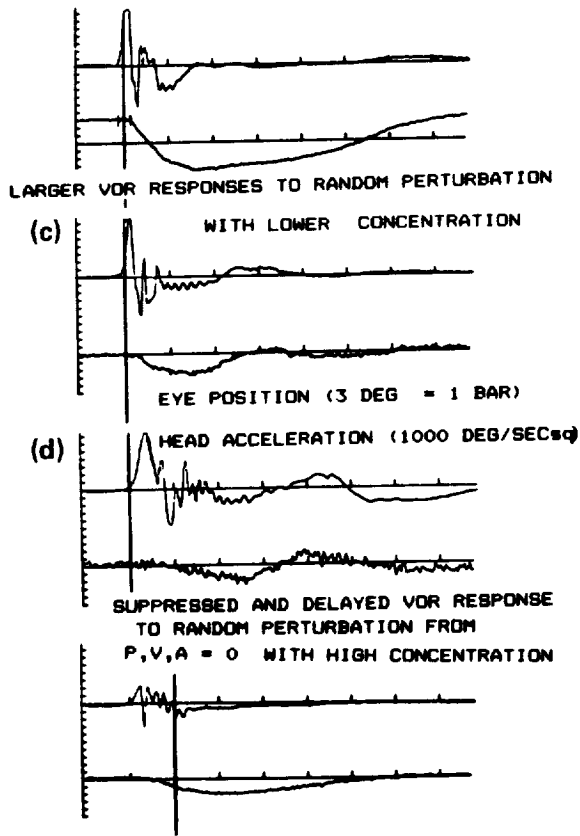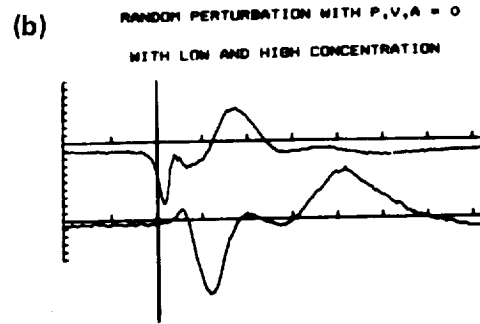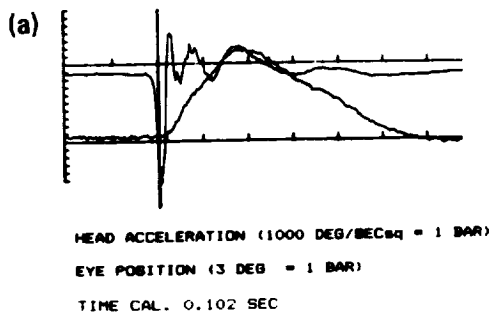b) Explanatory scheme for the continual change of gaze types (lower).

(a)

HEAD ACCELERATION (1000 DEG/SECsq = 1 BAR)

EYE POSITION (3 DEG = 1 BAR)

TIME CAL. 0.102 SEC

(b) RANDOM PERTURBATION WITH P,V,A = 0

WITH LOW AND HIGH CONCENTRATION

(e) PASSIVE ACCELERATION FROM ZERO VELOCITY

3

0 → TIME

-3 0.1 SEC

LARGER VOR RESPONSES TO RANDOM PERTURBATION

WITH LOWER CONCENTRATION

20 DEG
20 DEG   LOW INTENT
0 DEG → t

-20 DEG

HEAD ACCELERATION (1000 DEG/SECsq)

(c)

EYE POSITION (3 DEG = 1 BAR)

HEAD ACCELERATION (1000 DEG/SECsq)

(d)

INTERMEDIATE INTENT

15 DEG

EYE POSITION

SUPPRESSED AND DELAYED VOR RESPONSE
TO RANDOM PERTURBATION FROM
P,V,A = 0   WITH HIGH CONCENTRATION

MAXIMAL INTENT

10 DEG

Figure 2.– Random perturbation from primary position. (a) Low and (b) very high intent. Random perturbation from primary position, (c) low and (d) very high intent. Random perturbation from primary position, explanatory scheme (e).
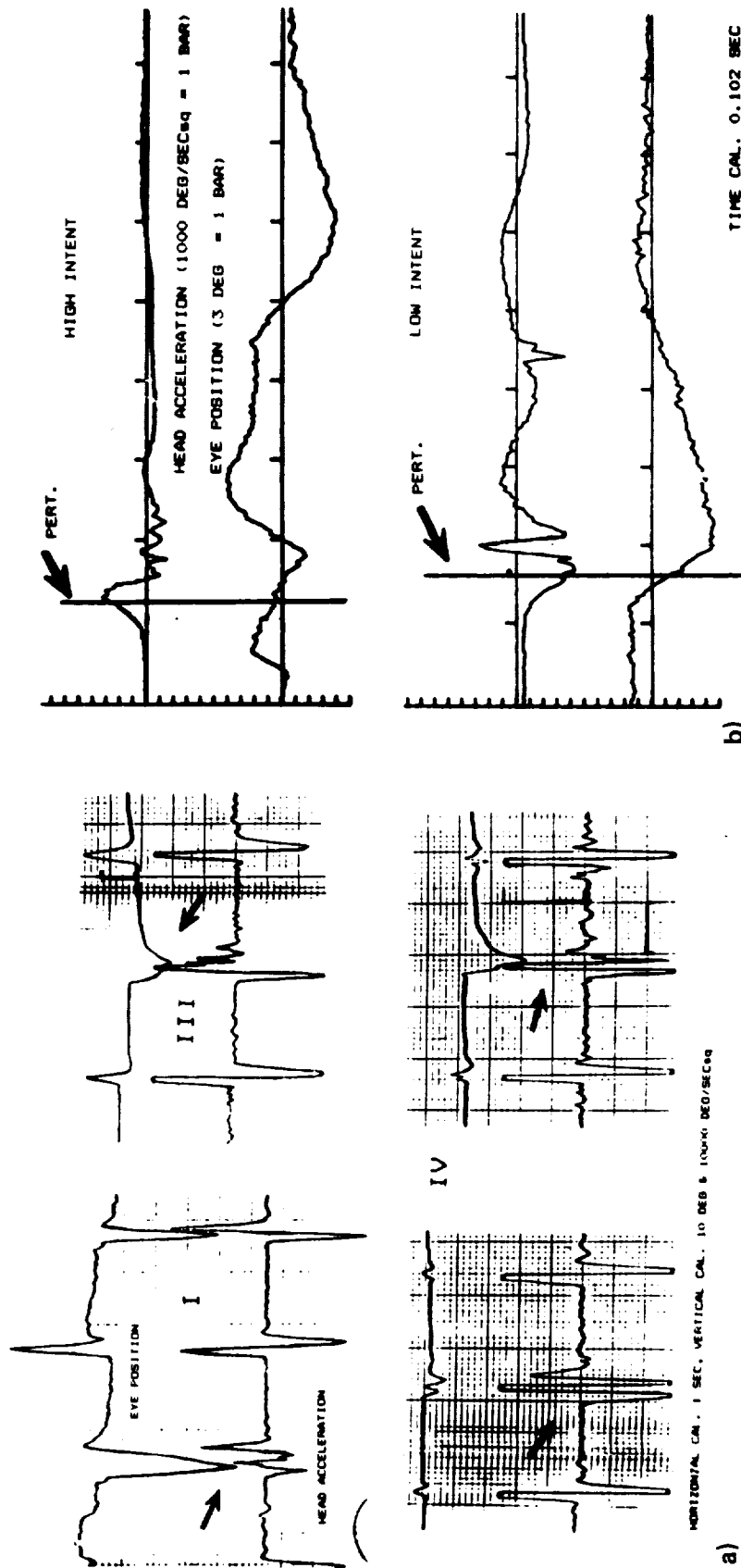
Figure 3.– a) Random perturbation of gaze type 1, 3, 4 in flight (arrows; left). b) Random pertur-
bation of gaze type 3 with high (upper) and low (lower) intent (right).
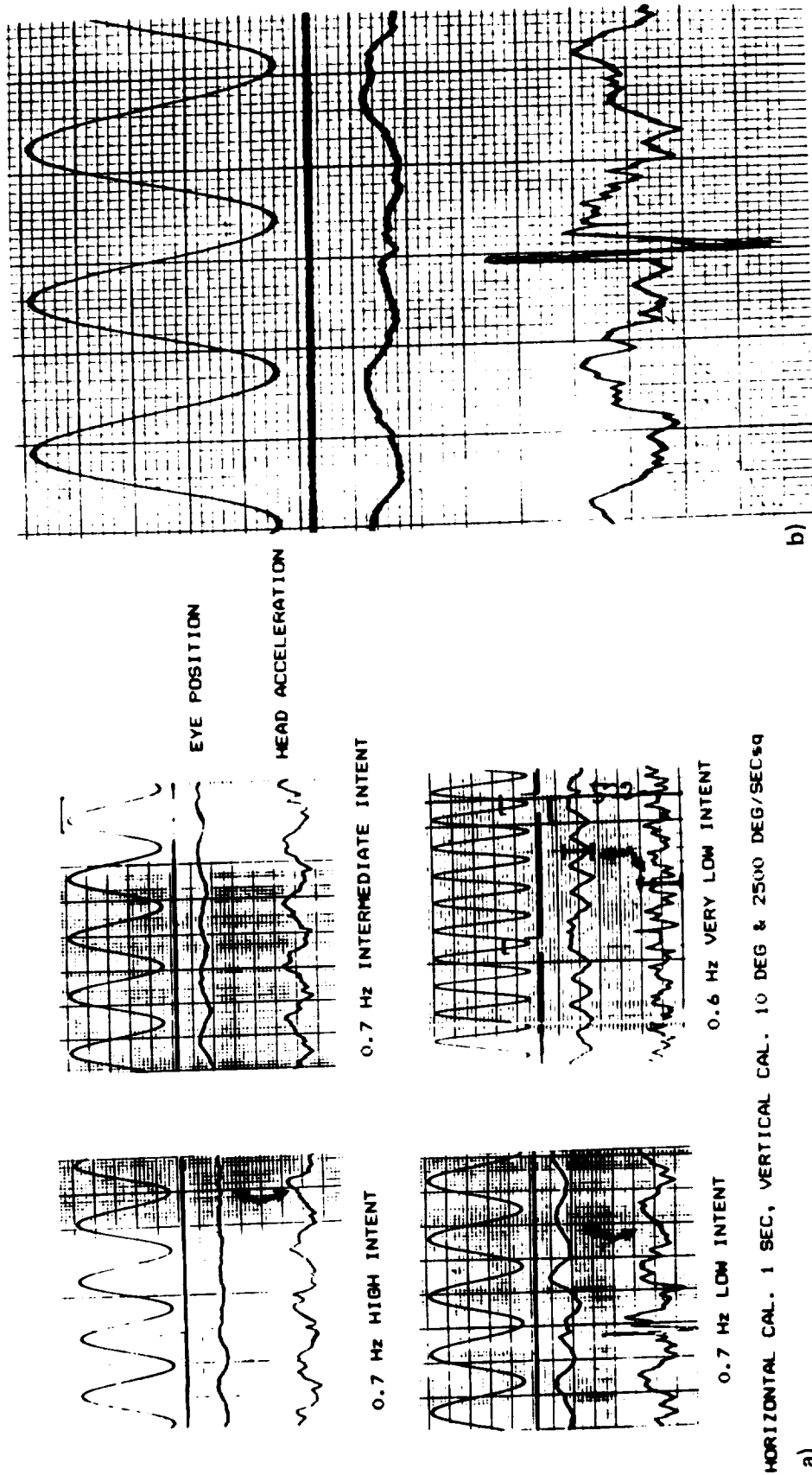
Figure 4.– a) Variable amount of fixation suppression of VOR as a function of intent (left).
b) Random perturbation of coordinated gaze pursuit: suppressed VOR response (middle).