though more variable, largely confirm two of the findings of Hirsch and Spinelli (*4*): (i) About half of the 350 cells studied were either unresponsive, poorly and erratically responsive, or nonselective in their responses to visual stimuli. (ii) The majority of the remaining selective units were monocularly driven and preferred orientations near the one to which the effective eye had been exposed. These results will be reported in full elsewhere.

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9. An exception to this is the study by Hirsch and Spinelli (*4*), who mapped elongated receptive fields by computer for 32 cells in nine cats. Because they inferred best orientation from receptive field shape and plotted receptive fields using horizontally or vertically moving spot stimuli, their results are not directly comparable to conventional plots.
10. The only published report of an experiment using a blind procedure is a study of one animal by Pettigrew *et al.* (*5*).
11. C. Blakemore, personal communication.
12. A light lock was used so that the room was always dark, and the system was tested with occasional 24-hour exposures of Tri-X film.
13. An exception to this procedure was H-4, whose eyes were sutured shut before opening and remained so until he was placed in the dark room at 47 days of age.
14. A ruff was a section of a 130° cone which prevented the kitten from seeing its own body.
15. Stripes ranged between 0.6 cm and 10 cm in width, and the kitten was free to move around the glass plate. The floor of the cylinder was black matte. A 32-watt Cool White fluorescent tube and several layers of diffusers provided uniform illumination across the ceiling of the cylinder. Halfway up the cylinder the white stripes were 153 cd/m^2 and the black stripes were 9.4 cd/m^2.
16. Subject H-4, which had no littermate, was the only one whose orientation exposure was known during the recording experiment.
17. The bar was of optimal length and width and was swept at optimal velocity as determined from stimuli moved by hand.
18. We think that analysis in terms of regularly spaced sites provides more information about the preferred orientations represented in a region of cortex than an analysis limited to well-isolated unit responses. Isolation of a single cell's activity at a given site depends to a great extent on electrode characteristics, and failure to isolate a single cell probably does not reflect an absence of responsive cells near that site. Probably because neighboring cells have similar preferred orientation (*8*), simultaneously recorded responses from several cells usually show a well-defined orientation preference.
19. Orientation selectivity (the width of the orientation-tuning function) was considered only for response histograms compiled from well-isolated unit responses. In addition, there was no tendency for units whose preferred orientations were near the exposed orientation to be more frequently encountered earlier in the recording experiment than later.
20. We thank Professor P. Schiller for his generous instruction, moral and technical support, and criticism. We also thank A. Polit for his excellent computer programs, and K. Anderson for her secretarial help. These experiments were made possible by a predoctoral training grant to H.-L. Teuber (NIH 5 TO1-GM010164-13) and grants to P. H. Schiller from NIH (EY00676).

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21 April 1975

Perceived Visual Motion as Effective Stimulus to Pursuit Eye Movement System

Abstract. *Human eye tracking of a foveal afterimage during angular head oscillation in the dark produced smooth eye movements exceeding those for normal vestibular nystagmus, and a reduction in the frequency of the fast phase component of nystagmus eye movements. These results may support a closed loop extension of the corollary discharge theory, with oculomotor commands based on perceived object velocity.*

The relative stability of the visual world during voluntary eye movements is a classical problem in psychophysics (*1*). The debate has centered around inflow (proprioceptive feedback) versus outflow (efferent copy, Helmholtz's effort of will, corollary discharge) explanations to account for compensation of the influence of eye movements upon retinal image motion. Psychophysical evidence involving active or passive eye movements tends to support the outflow theory (*2*). The control of eye tracking movement has more recently been studied from the servomechanical point of view, where the emphasis of experiments and cybernetic models has been on the causal relationships between the target motion or retinal motion and the resulting saccadic and pursuit eye movements (*3*). The need to relate the new (objective) and old (subjective) studies has been recognized (*4*). Might not the perceived target motion (rather than the actual target motion) be utilized for generating eye movement commands? This possibility, raised independently by Heywood (*5*) and by Rashbass (*6*) and Robinson (*7*) in interpreting the eye tracking model of Young *et al.* (*8*), is examined here through an experiment involving afterimage tracking during vestibular stimulation.

The experiment is intended to test the

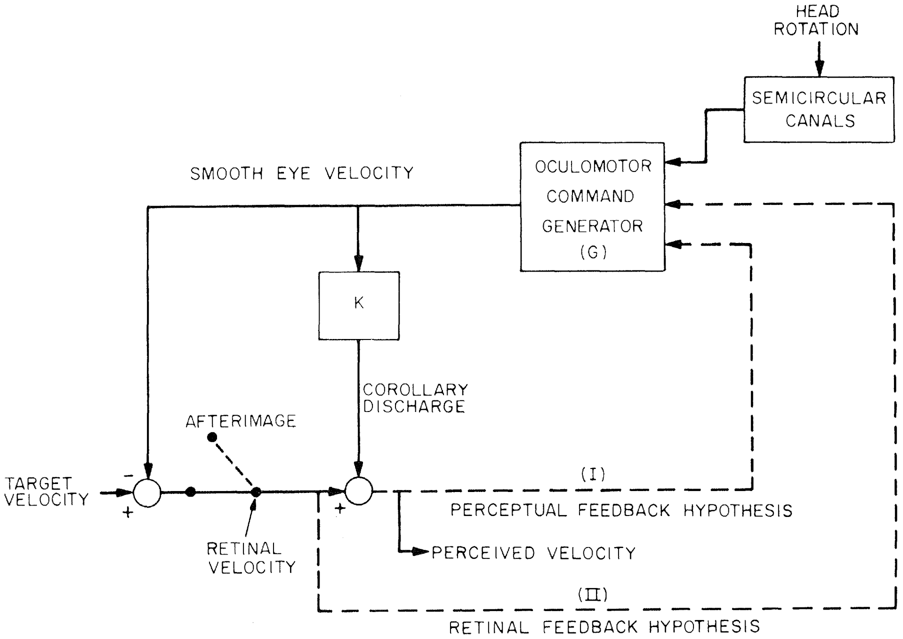

Fig. 1. Compensation by corollary discharge for the eye movement effect on the retinal image motion. In this experiment the input is from head rotation. Tracking a foveal afterimage rather than an external target opens the retinal feedback loop and activates only the internal positive feedback loop that results from connecting the corollary discharge with the postulated perceptual feedback path; *G*, open loop gain of vestibulo-ocular reflex arc; *K*, gain of corollary discharge path.

hypothesis of a feedback loop from perceived target velocity to smooth eye movement. This "perceptual feedback hypothesis" is indicated by broken line I in Fig. 1. As a means of generating smooth eye movements without any possible feedback from retinal velocity or from perceived target motion, we stimulated the vestibular system by passive sinusoidal rotation in the dark. It was then necessary to generate a visible target that could be perceived as moving relative to the observer but would produce a stationary retinal image. A small foveally centered afterimage served to stimulate loop I, but not loop II, the retinal slip feedback path. During subject rotation, the afterimage, remaining stationary on the retina, nevertheless appears to move relative to the subject (*9*). The influence of this perceived target motion on vestibular nystagmus during the forced visual tracking is evidence supporting the perceptual feedback hypothesis.

Four subjects were rotated about a vertical axis in the dark, head maintained erect by means of a Barany-type rotating chair and cabin. The frequency of oscillation was varied randomly in the range 0.025 to 0.7 hertz. Peak angular velocity was also varied, but never exceeded 40 deg/sec. To produce brisk nystagmus, alertness was maintained by having subjects perform mental arithmetic. After several cycles of oscillation in the dark to establish a steady pattern of vestibular nystagmus, a fixation point was lighted and a small monocular foveal afterimage was produced on the right eye by a flashbulb behind an aperture. Subjects were instructed to fixate the target and indicate its direction of motion with a three-position switch. [Kommerell and Täumer (*10*) showed the importance of attention in directing afterimage tracking.] Movements of the right eye were monitored continuously with a pulsed infrared photoelectric monitor.

A typical recording is shown in Fig. 2. The eye movement pattern during initial rotation in the dark at 0.25 hertz shows normal vestibular nystagmus, with slow phases compensating for chair motion and with regular return fast phases. This is clearly seen in the cumulative eye position, which is a computer-reconstructed sum of all slow phase movements (*11*). Following delivery of the flash and appearance of the afterimage, the fast phase of nystagmus is almost entirely absent, and the eye movement resembles tracking of sinusoidal target motion. The amplitude of the slow phase component of the roughly sinusoidal eye movement pattern is markedly increased, and there is a slight preponderance of movement to the right, as seen in the cumulative eye position trace. The phase lag of smooth eye movement velocity relative to the chair velocity is less during afterimage tracking than during vestibular nystagmus in the dark. Direction of apparent motion of the afterimage relative to the observer is in phase with the eye movement, as expected from the corollary discharge theory. In summary, chair rotation to the left causes a slow-phase compensatory eye movement to the right. The afterimage, which is stationary on the retina, appears to move to the right during the slow eye movement. Finally, in support of the perceptual feedback hypothesis, the perceived target motion to the right produces further slow eye movement to the right, resulting in an increase in amplitude of the observed eye movement.

In the last part of the sample record, as the afterimage fades and is no longer seen, the eye movement pattern returns to the initial pattern of vestibular nystagmus in the dark. For the four subjects tested, the frequency response of the vestibulo-ocular reflex relating cumulative eye velocity to chair velocity is given in Table 1. As com-

Table 1. Amplitude ratio and phase lag of smooth eye movement relative to sinusoidal head rotation. Eye movement during afterimage tracking is compared to the slow phase of vestibular nystagmus in complete darkness without afterimage. Four subjects were studied; S.D., standard deviation.

Frequency (hertz)	Amplitude ratio (db)				Phase lag angle, eye velocity relative to chair velocity (deg)			
	No afterimage		Afterimage		No afterimage		Afterimage	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
0.025	-2.10	1.60	-0.54	2.33	145.8	19.8	111.3	18.5
0.06	-3.77	2.21	-0.02	0.97	173.2	15.7	133.3	10.6
0.10	-3.99	2.05	-1.71	2.05	180.0	15.1	159.7	10.0
0.25	-2.88	2.24	1.06	1.45	173.5	10.1	158.5	4.2
0.50	-2.75	1.81	2.95	2.28	179.8	11.6	169.3	7.2
0.70	-1.77	0.38	3.15	2.28	166.5	17.5	158.3	9.0

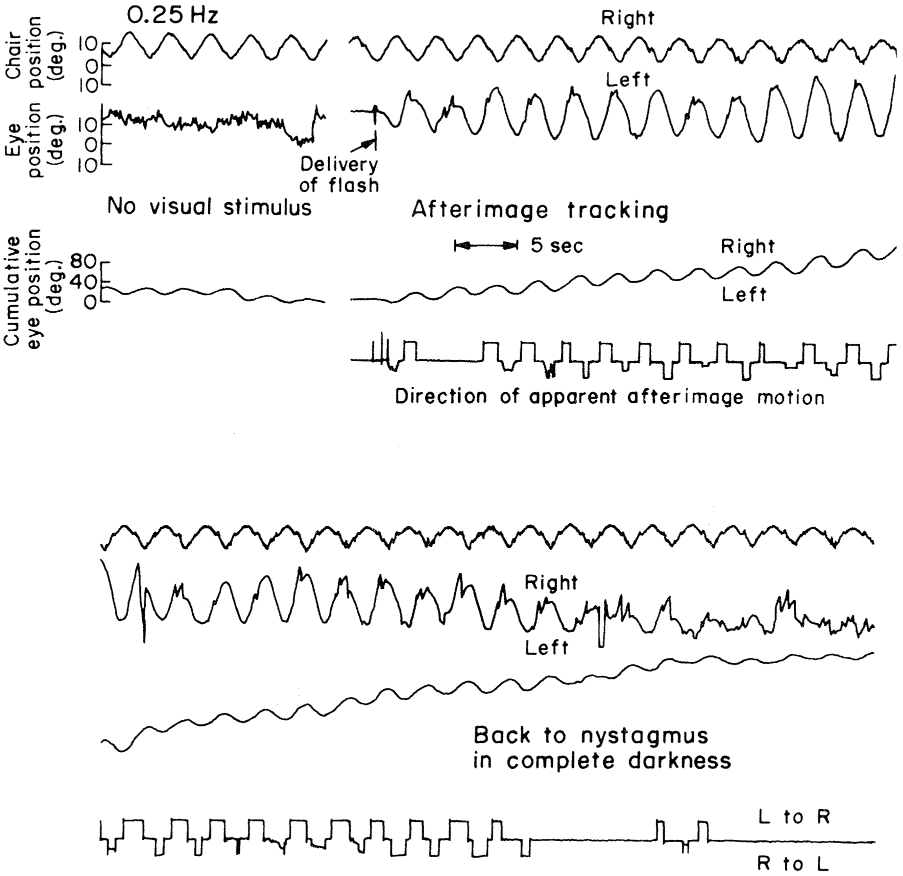

Fig. 2. Sample record for one subject at the oscillation frequency of 0.25 hertz. During the afterimage tracking, note (i) the tendency toward disappearance of the fast phase component of nystagmus; (ii) the essential agreement between direction of apparent motion of the afterimage and the direction of smooth eye movement; and (iii) the amplitude increase of the smooth eye movement as compared with the nystagmus slow phase in complete darkness.

pared to the no-afterimage case, afterimage vestibular response has significantly higher gain and lower phase lag over the range tested ($P < .05$). Similar effects were seen for the vestibulo-ocular frequency response when aperiodic motion was studied, with and without an afterimage (*12*). This difference between the dark and afterimage tracking cases supports the perceptual feedback hypothesis.

The observation that fast phases are virtually eliminated by a foveal afterimage supports the interpretation that the overriding information used for saccade generation is displacement of the target image from the foveal threshold (*13*). The increase in amplitude of the slow phase during afterimage tracking may imply the existence of a positive feedback loop not present during rotation in the dark. With path II in Fig. 1 open (no retinal motion), the remaining feedback (path I) is positive. Any perceived target motion generates a smooth eye movement in the same direction, presumably of the same velocity ($G = 1$ in Fig. 1). Corollary discharge, in the absence of any retinal feedback, results in a new perceived target velocity in the direction of the eye movement, and with velocity K times that of the eye and the original perception. Since the system is stable (no runaway pursuit instability is seen in afterimage tracking), the positive feedback loop must have gain less than unity ($K < 1$). On the other hand, the corollary discharge theory would require that $K = 1$ so that the stability of the perceived world is maintained during eye movements. The perfect cancellation implied by $K = 1$ would indicate that eye movements have no net effect on perceived target velocity in normal tracking, and would effectively open the feedback loop.

A possible explanation is that the corollary discharge gain is less than unity—that compensation for pursuit tracking is only partial, as may be observed by noting the apparent motion of a stationary background during fast pursuit tracking of a target. Supporting this explanation is the experiment of Dichgans *et al.* (*14*) showing that the subjective velocity of a moving visual target is about 1.6 times greater when viewed by stationary eyes (retinal motion only) than when tracked with pursuit motion. This suggests that the corollary discharge accounts for only about 63 percent ($K = 1/1.6$) of the retinal image motion associated with smooth eye movement, and that the slow phase amplitude in our foveal afterimage experiment should increase to as high as 2.5 times the value for vestibular nystagmus in the dark. Under normal tracking, the system remains effectively under negative feedback control while retaining the essential function of corollary discharge for perception (*15*). Partial cancellation might also account for the oculogyral illusion, the apparent motion of a real, head-fixed target during vestibular stimulation. Despite attempts at visual fixation, some vestibular nystagmus persists. The motion illusion is in the direction opposite to the slow phase component (in contrast to the case in afterimage tracking), which indicates incomplete compensation for the slow eye movement.

Finally, there are two alternative explanations for the current results which cannot yet be dismissed. (i) The removal of the fast phase of nystagmus may have eliminated a mechanical interaction between the phases (*16*). (ii) The presence of a visual stimulus (afterimage) in itself may have raised the level of subjective attention and increased the gain in the vestibulo-ocular reflex arc. In this regard, it should be recalled that increase in attention by other means and attempts to stare straight ahead increase the vestibulo-ocular gain.

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15. The gain for semicircular canal output to smooth eye velocity, from Fig. 1, is G for vestibular nystagmus in the dark, $G/[1 + (1 - K)G]$ for normal tracking, and $G/(1 - KG)$ for afterimage tracking. Assuming that $G = 1$ and $K = 0.6$, the slow phase velocity amplitude ratio should be $1/(1 - 0.6) = 2.5$, or 8 db higher with afterimage tracking than with no vision, which is somewhat greater than the observed shift. Normal eye tracking remains under negative feedback. Caution must be exercised in assigning quantitative loop gains, however, as these gains show adaptive changes when the external visual feedback is changed to open loop tracking [G. Vossius, *Prog. Cybern.* **2**, 111 (1965)].
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23 August 1974; revised 8 September 1975

Spout of the Gray Whale: Its Physical Characteristics

Abstract. *In a calm lagoon of Baja California the spout or blow of adult and young gray whales,* Eschrichtius robustus, *was observed. Of three calves the maximum flow rate was 200 liters per second, and the duration of both expiration and inspiration was slightly less than 1 second. Gas passes through the external nares at 44 meters per second during inspiration and four to five times this rate during expiration. At this latitude the whale's spout consists mainly of seawater blown up during expiration.*

Every year from December through March a remarkable biological phenomenon attracts much attention in Southern California. It is the nearshore migration of the gray whale, *Eschrichtius robustus*, on its way to calve and breed in or near the lagoons of Baja California, Mexico. Little is actually seen of the whale, but all observers, amateur or professional, can easily see the product of its unique mode of breathing, the spout.

In late January and early February we took advantage of the whales being in the calm water of the lagoons to observe and make a refined examination of the timing and structure of the spout. During this period we had the opportunity to capture and hold calves in shallow water for periods of