pected, irrelevant stimulus changes (*21*), and so forth. In this regard, P3 can be considered to index the relative timing of stimulus evaluation between experimental conditions (*1, 21*), independent of RT. But our results suggest that P3 can be used to assess the temporal occurrence of stimulus evaluation because it is related in time to N2.

The data and theoretical implications indicate that many of the hypotheses concerning the functional significance of the brain activity P3 reflects (*22*), such as target selection (*2*), are more appropriately regarded with respect to N2 (*5*). More recent hypotheses (*23*) conceptualize P3 as reflecting brain activities concerned with future events, since P3 often occurs too late to be involved in the behavioral responses related to the eliciting stimulus. Understandably, P3 has received more attention from investigators than N2; it is larger in amplitude and therefore more readily observed and measured, whereas N2 is not only smaller but is also often obscured by P2 (Fig. 1). Whereas P3 can index the relative timing of stimulus evaluation between conditions, however, N2 can more directly measure the absolute timing of certain decision processes.

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9. Endogenous ERP's are potentials that are more related to psychological states of the subject, in contrast to exogenous ERP's which are more related to stimulus parameters. The ERP components elicited by randomly omitted stimuli constitute the clearest examples of endogenous potentials.
10. H. Bostock and M. J. Jarvis, *Electroencephalogr. Clin. Neurophysiol.* **29**, 137 (1970).
11. The P2 latency was essentially constant, similar to the results of (*4*), in contrast to increases in latency of both P2 and N2 with longer RT reported by Bostock and Jarvis (*10*) and R. Parasuraman and D. R. Davies [*Percept. Psychophys.* **17**, 465 (1975)]. On the other hand, E. Donchin and D. B. Lindsley [*Electroencephalogr. Clin. Neurophysiol.* **20**, 217 (1966)], L. Morrell and F. Morrell [*ibid.* **20**, 567 (1966)], R. T. Wilkinson and H. C. Morlock [*ibid.* **23**, 50 (1967)], and D. Friedman, H. G. Vaughan, Jr., and L. Erlenmeyer-Kimling [*ibid.*, in press] found that P2 remains constant in latency despite changes in RT.
12. Of the trials accepted for statistical analysis, only one had an N2 latency greater than 400 msec and fewer than 10 percent had a latency between 300 and 400 msec.
13. For example, when combined across subjects and conditions, N2 was scored on 14 of 81 trials with RT's between 180 and 295 msec, whereas N2 was scored on 136 of 260 trials with RT's between 300 and 415 msec.
14. The P3 and RT means were taken from table 2 of (*4*).
15. For each subject in the two conditions, the mean and standard deviation of N2, N, and P values for two-tailed t-tests, respectively, were: J.K. (easy) 207 ± 45, 20; (hard) 245 ± 37, 12, $P < .05$. W.R. (easy) 239 ± 50, 20; (hard) 271 ± 51, 15, $P < .05$. R.S. (easy) 234 ± 20, 34; (hard) 254 ± 39, 32, $P < .10$. S.V. (easy) 252 ± 47, 22; (hard) 319 ± 77, 14, $P < .001$.
16. The correlation coefficients and their two-tailed P values were: J.K. (easy) .88, $P < .001$; (hard) .61, $P < .05$. W.R. (easy) .89, $P < .001$; (hard) .74, $P < .001$. R.S. (easy) .30, $P > .05$; (hard) .64, $P < .001$. S.V. (easy) .74, $P < .001$; (hard) .85, $P < .001$.
17. See table 3 of (*4*) for the correlations between P3 latency and RT on single trials.
18. For each subject and condition, the correlation coefficient, N, and two-tailed P values, respectively, were: J.K. (easy) .69, 14, $P < .01$; (hard) .53, 7, $P > .05$. W.R. (easy) .63, 18, $P < .01$; (hard) .93, 9, $P < .01$. R.S. (easy) .36, 24, $P > .05$; (hard) .63, 27, $P < .01$. S.V. (easy) .52, 18, $P < .05$; (hard) .83, 12, $P < .01$.
19. There are several reasons for believing that the N2 studied in this report is not a negative wave associated with motor potentials (MP's) that precede motor responses [L. Gilden, H. G. Vaughan, Jr., L. D. Costa, *Electroencephalogr. Clin. Neurophysiol.* **20**, 433 (1966)]. (i) In our previous experiment (*4*), a control condition in which subjects performed the finger movement in a self-paced manner revealed no observable MP's; (ii) in the same experiment the EEG was averaged with respect to the pulse generated by each subject in each condition by the finger lift, performed in response to targets, which revealed no observable premovement MP's (the lack of observable MP's was presumably related to the use of a small finger movement deliberately chosen to minimize MP's); (iii) negative-going MP's preceding large, vigorous hand movements are usually small in amplitude at the vertex, generally about 2 to 4 μV, whereas the N2 for the longer RT's in Fig. 1 are much larger.
20. See C. C. Duncan-Johnson and E. Donchin [*Psychophysiology* **14**, 456 (1977)] for a compatible view.
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24. Supported by PHS grants HD 10804, MH 06723, and core grant HD 01799.

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Smooth Pursuit Eye Movements: Is Perceived Motion Necessary?

Abstract. *It has recently been shown that perceived motion, in the absence of any appropriate retinal motion, is a sufficient stimulus to generate smooth pursuit eye motions. This raises the question of whether perceived motion is necessary for pursuit. In three experiments we obtained a negative answer to this question: retinal motion always governed pursuit.*

When a moving object enters the visual field, it is frequently followed by the eyes with a slow smooth motion distinctly different from the rapid ballistic eye motions known as saccades, which serve to change the eyes' point of fixation. Rashbass (*1*) presented evidence supporting the traditional viewpoint that the stimulus for these slow eye motions is the movement of an image over the retina. Recently, however, investigators have begun to argue that it is not retinal motion but rather the perceived motion of a stimulus that is a condition for smooth pursuit (*2*). There is now evidence that the eye can engage in smooth pursuit when there is perceived motion of a target in the absence of any appropriate retinal motion. It has not thus far been demonstrated, however, that perceived motion is actually necessary for pursuit. Two relevant questions to be answered are (i) whether pursuit eye motions can be elicited when there is retinal motion but no perceived motion and (ii) whether the smooth pursuit response of the eye will be to the retinal or perceived motion of a target in a situation in which there is a conflict between the two. Answers to these questions should reveal the relative importance of perceived and retinal motion in driving the pursuit system.

We now report the results of three experiments which address these questions. In one of these the pursuit behavior of the eye was examined for a set of stimulus velocities which ranged from well below to well above our subjects' detection thresholds. In the second, the addition of a stationary frame of reference could be used to render visible the slowest of these velocities, and a moving frame of reference could be used to induce the perception of motion in a stimulus which was in fact stationary. In the third experiment, eye movements were examined under conditions in which the phenomenon of induced motion was used to create a conflict between the direction of a target's retinal motion and the perceived direction of its motion.

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In all the experiments the stimulus display was multiplexed onto a fast phosphor cathode-ray tube 2 feet in front of the subject; the display was all that was visible to the subject. Eye motions were monitored with a Double-Purkinje image eyetracker (*3*) with a noise level that was typically less than 5 minutes of arc and recorded with an analog chart recorder for subsequent analysis. In each experiment, mean data for three subjects are presented.

In experiment 1, a single point of light was moved either left or right for 2 seconds at velocities of 3, 6, 9, 12, or 15 minutes of arc per second. There were nine trials of leftward and nine of rightward motion for each stimulus velocity and 30 zero-motion trials. The total set of 120 trials was administered according to a predetermined randomized design.

Prior to each trial, the subject was light-adapted for 10 seconds in an effort to minimize autokinetic motion. Following this there was 10 seconds of darkness, after which the stimulus appeared on the cathode-ray tube. In this and in all subsequent experiments, the subject was instructed to fixate the target stimulus and to follow it with his eyes if it moved. When the eyetracker indicated proper fixation, the experimenter announced "ready" and initiated the stimulus movement. The stimulus vanished after 2 seconds, and the subject reported whether it had moved left or right. In experiments 1 and 2, a forced choice procedure was followed.

We were primarily interested in whether the tendency to pursue the motion of the stimulus would develop as a function paralleling the subject's increasing ability to detect and report stimulus motion. All eye records were analyzed by measuring the total change in horizontal eye position from the start to the end of the stimulus motion interval, and by subtracting out the measurable saccadic contribution to obtain an estimate of slow pursuit. We believe our records allowed us to dependably detect all saccades which were 3 minutes of arc or larger (Fig. 1A).

As was expected, the accuracy of motion detection increased from near chance to largely correct as the stimulus velocity increased (Fig. 2). A 75 percent criterion threshold falls just above 9 min/sec, which is in agreement with earlier research (*4*). The following response of the eye, however, is near optimum at the slowest stimulus velocity and remains at a high level for all other velocities (*5*). Thus, it seems that pursuit motion of the eyes is not dependent on the perception of motion. The data support this conclusion even if only trials in which the subjects incorrectly report the direction of motion are considered.

Since the eye tracks almost perfectly when stimulus motion is well below threshold, making that slow motion perceptible does not seem likely to alter the tracking response. This was confirmed in experiment 2. Of greater interest is the fact, ascertained in experiment 2, that if a motion is induced in a stationary target, the eye holds a nearly stable fixation despite the perceived apparent motion. This should not be the case if the primary stimulus for pursuit is perceived motion. This experiment had three conditions. The first was a replication of the 3 min/sec condition of the previous experiment. In the second condition, the target motion of 3 min/sec was made perceptible by virtue of a surrounding stationary frame consisting of four points which marked the corners of a rectangle 3° high and 0.5° wide. In the last condition, the target remained stationary while the frame moved left or right for 2 seconds at 3 min/sec, inducing an apparent opposite motion in the stationary target.

The stimulus array was effective in inducing motion in the stationary target in condition 3 and in making the target motion perceptible in condition 2 (Table 1). As expected, the pursuit behavior of the eye is not better in condition 2, the object-relative condition, in which the frame is present and target motion is consistently perceived, than in condition 1, the subject-relative condition, in which the target is all that is visible and in which its motion is not detected. Furthermore, despite the apparent and slight tendency of the eye to drift in the direction of the induced motion in condition 3,

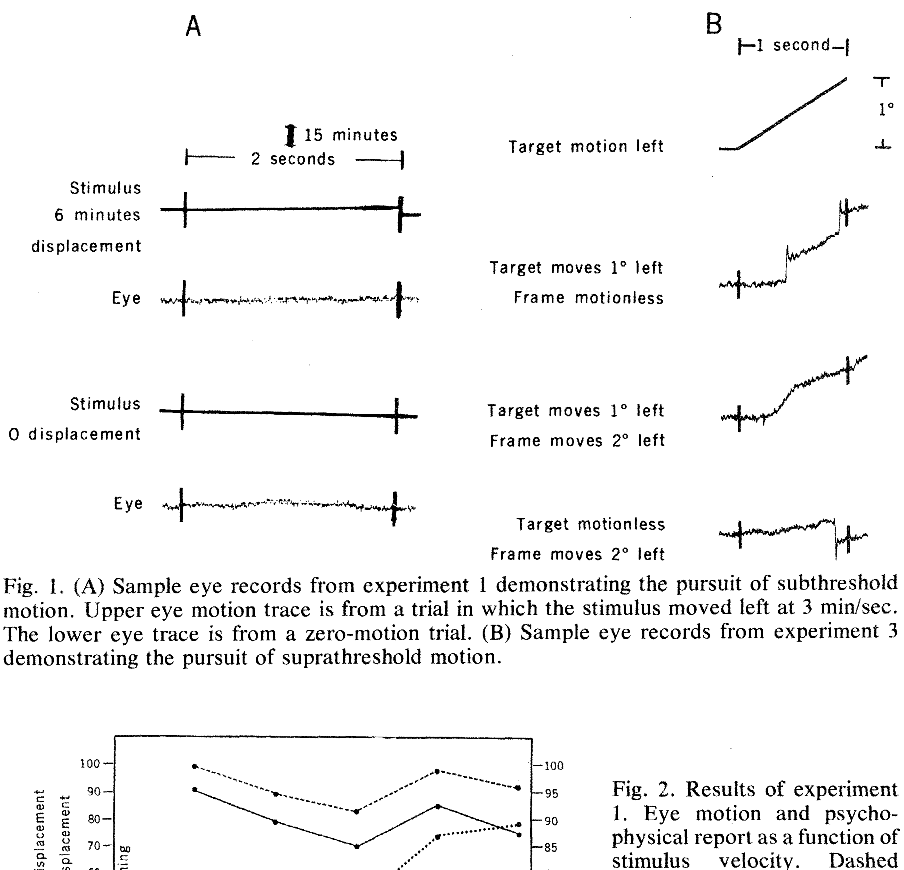

Fig. 1. (A) Sample eye records from experiment 1 demonstrating the pursuit of subthreshold motion. Upper eye motion trace is from a trial in which the stimulus moved left at 3 min/sec. The lower eye trace is from a zero-motion trial. (B) Sample eye records from experiment 3 demonstrating the pursuit of suprathreshold motion.

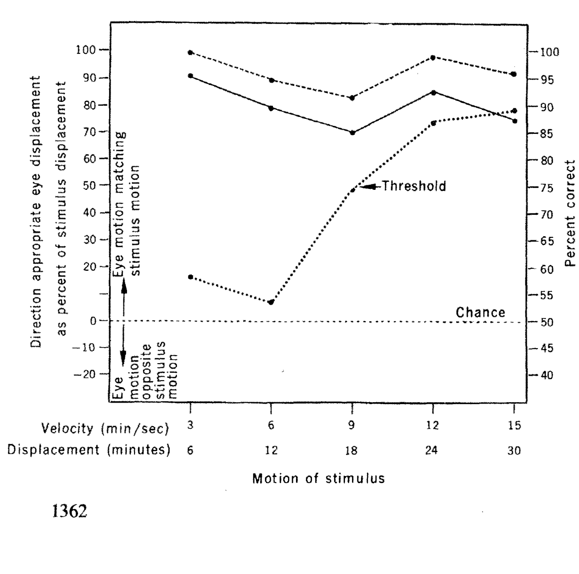

Fig. 2. Results of experiment 1. Eye motion and psychophysical report as a function of stimulus velocity. Dashed line, total change in eye position; solid line, slow pursuit component in eye position change; dotted line, percent correct in psychophysical report of direction. Eye motions are plotted against the left ordinate as a percentage of total stimulus displacement. Psychophysical reports are plotted against the right ordinate.

the drift is small (less than 1 minute), and is primarily attributable to one subject. Thus, it seems that when there is a conflict between retinal and perceived motion, the retinal information exerts primary control over the pursuit system.

This conclusion is supported by the results of a third experiment, which, unlike the first two, involved suprathreshold motion; we can thus generalize our conclusion to tracking velocities well outside the slow-drift range and well within the normal range of smooth pursuit. The display, slightly altered from the previous experiment, consisted of the target point surrounded by a 6° by 1° rectangular array of six points. The two additional points marked the midline of the rectangle and were aligned with the target. There were three conditions: (i) the frame was stationary and the target moved left or right at 1° per second, which resulted in simple object-relative motion; (ii) the target moved left or right at 1° per second for 1 second while the frame moved 2° per second in the same direction, which resulted in an induced motion of the target in the direction opposite its real motion due to its displacement relative to the frame; and (iii) the target was stationary and the frame moved 2° per second for 1 second, which also frequently produced an induced motion of the target opposite the frame. At the end of each trial, the subject reported whether the target appeared to move left or right, or remain stationary.

The psychophysical data indicate that 98 percent of target motion reports in condition 1 were veridical, while in condition 2, 100 percent of the reports were of induced motion, and in condition 3, 77 percent of the reports were of induced motion. The data on eye movements are consistent with those of the slow-velocity experiments. A comparison between condition 1, in which there was simple object-relative motion, and condition 2, in which an induced motion caused the moving target to appear to be moving in the opposite direction, reveals that the total displacement of the eye is similar (50.11 minutes and 47.47 minutes). The slow-pursuit component of that displacement is, if anything, slightly greater in condition 2 (38.72 minutes as opposed to 32.13 minutes) (*6*). This is so despite the consistent reports from all observers that the motion of the target was opposite its real motion in this condition. Thus while object-relative displacement determined the direction of the perceived motion, retinal motion determined pursuit.

Table 1. Mean direction appropriate eye motions and psychophysical reports (experiment 2). In condition 1 the target motion is subject-relative, in condition 2 it is object-relative, and in condition 3 it is induced. In the eye motion data, a + indicates eye motions in the same direction as stimulus motion, and a − indicates eye motion opposite stimulus motion. The numbers are eye movements in minutes of arc. A +6 would indicate a perfect following response in the subject-relative and object-relative conditions, while a 0 would represent perfect fixation in the induced motion condition. In the psychophysical report data, the percentages of veridical reports are given for condition 1 and condition 2, and the percentage of induced reports is given for condition 3. The subjects' mean confidence ratings are on a scale from 1 (indicating certainty) to 3 (indicating a guess).

Condition	Total eye movement	Slow drift	Psychophysical reports	
			Correct (%)	Confidence rating
1	+5.06	+5.17	52	2.125
2	+4.64	+4.55	99	1.08
3	− .8	− .76	99	1.17

Figure 1B illustrates characteristic eye records of one subject in the three conditions. The tendency for the eye to drift in the direction of frame movement in condition 3 in which the target was stationary, which was typical of the eye records of all our observers, is apparent in the sample eye record. This tendency was evident regardless of whether an induced motion of the target was reported. No tendency to pursue the perceived induced motion was noted in any subject who reported induced motion.

Taken together, the results demonstrate that retinal displacement in the absence of perceived motion is an adequate stimulus for pursuit; thus, perceived motion cannot be considered necessary for pursuit. Moreover, in instances in which retinal and perceived motion conflict, pursuit is controlled by retinal and not by perceived motion. This is so both for very slow stimulus motion as well as for stimulus motions well within the range of normal tracking. These data are not incompatible with the view that smooth pursuit movements are predominantly under subcortical control. The findings of other investigators (*2, 3*) suggest that in the absence of a conflict between retinal and perceived motion, perceived motion may control pursuit, but our data indicate that the power of perceived motion to drive the pursuit system is limited and confined to such nonconflict situations.

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5. This is consistent with earlier reports concerning the ability of the eyes to track very slow motion [A. Yarbus, *Eye Movements and Vision* (Plenum, New York, 1967)].
6. A consistent difference between the eye records from conditions 1 and 2 is intriguing. In condition 1, where there was simple object-relative motion of the target, there were more saccades evident than in condition 2, where perceived and retinal motion were in conflict (Fig. 1B).
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The Dodo and the Tambalacoque Tree

I do not dispute that coevolution between plant and animal exists and that the germination of some seeds may be assisted by their passing through the gut of animals. However, that "mutualism" of the famous dodo and *Calvaria major* (tambalacoque) is an example (*1*) of coevolution is untenable for the following reasons.

1) *Calvaria major* grows in the upland rain forest of Mauritius with a rainfall of 2500 to 3800 mm per annum. The dodo according to Dutch sources roamed over the northern plains and the eastern hills in the Grand Port area—that is, in a drier forest—where the Dutch established their first settlement. Thus it is highly improbable that the dodo and the tambalacoque occurred in the same ecological niche. Indeed, extensive excavations in the uplands for reservoirs, drainage canals, and the like have failed to reveal any dodo remains.

2) Some writers have mentioned the small woody seeds found in Mare aux Songes and the possibility that their germination was assisted by the dodo or other birds. But we now know that these seeds are not tambalacoque but belong to another species of lowland tree recently identified as *Sideroxylon longifolium*.

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