Vision Research. Vol. 18, pp. 603–605

0042-6989/78/0501-0603$02.00/0

LETTER TO THE EDITORS

VELOCITY MATCHING DURING SMOOTH PURSUIT OF DIFFERENT TARGETS ON DIFFERENT BACKGROUNDS[1]

(*Received* 4 *May* 1977; *in revised form* 26 *August* 1977)

Human smooth pursuit is not completely understood. For example, its maximun average gain (eye velocity/target velocity) has been the subject of controversy. Studies of smooth pursuit of unpredictable ramps have given conflicting results. Puckett and Steinman (1969) and Steiman, Skavenski and Sansbury (1969) reported that maximum average gain was less than 1. Rashbass (1961) claimed that gain was equal to 1 under the same conditions. A resolution of this conflict is important because if the eye, on the average, lags behind the target, retinal slip velocity (the difference between eye and target velocity) could be used to keep the eye smoothly pursuing the target once smooth pursuit is underway.

Recent, interest in this problem was renewed by Robinson (1976, pp. 29–31) who suggested that there may be two smooth pursuit subsystems—0ne that uses retinal image slip to keep going and another that, on the average, matches eye velocity to target velocity.[2] This proposed velocity-matching "fast foveal" smooth pursuit subsystem, whose average gain would equal 1, uses retinal slip only to allow the eye to attain a velocity equal to target velocity. Once this velocity is attained it is "remembered" and used to keep the eye travelling at the same velocity as the target without any need for new retinal slip signals. Robinson proposed that such a fast foveal velocity-matching subsystem would be activated when motivation is provided to minimize velocity and position errors. Such motivation might arise when an acuity target is tracked because its critical detail would be hard to resolve if the target image slipped appreciably on the retina or if the target image moved away from the center of best vision in the fovea.

The present experiments set out to determine maximum average smooth pursuit gain under conditions designed to encourage the smooth pursuit subsystem to perform at its best. Specifically, smooth pursuit gain was measured while an acuity target (2 minimally separable bright points) was tracked against a lighted background by highly experienced subjects who had tracked this target almost daily for more than a month. Optimal performance was also encouraged by requiring the subjects to track a simple predictable target motion. We also measured smooth pursuit gain while they tracked a single point target against a dark and against a lighted background, and also the 2-point acuity target while it moved in a completely dark environment. These variations in the experiment were introduced in order to assess the importance of target type and background on smooth pursuit gain. It will be shown that target type and background do not affect the velocity of smooth pursuit, which can actually match the velocity of the target, providing its velocity is low, its motion simple and predictable, and the subjects highly practiced.

[1] This research was supported by Grant 00325 from the National Eye Institute. The computer time for this project was supported through the facilities of the Computer Science Center, University of Maryland.

[2] Attempts have been made to make similar kinds of distinctions in the past. Ter Braak (1936) distinguishes *Stier-Nystagmus* from *Schau-Nystagmus*. The former seems to be an involuntary slow reflexive eye movement used to maintain stability of the visual field, while the latter is a voluntary slow subsystem used to pursue small visual details. The distinction being made by Ter Braak resembles the contemproary distinction between OKN and smooth pursuit when they are believed to reflect the operation of two separate subsystems. Robinson (1976) is proposing a further distinction within the smooth pursuit subsystem.

METHOD

Horizontal movements of the right eye were recorded by a contact lens optical lever (Haddad and Steinman, 1973) whose sensitivity as used in the present experiment permitted resolution of eye position to better than 0.5′. The left eye was closed and covered and the head was supported by an acrylic dental biteboard.

The tracking target was either a single point or two points (separated vertically) which moved horizontally, either in complete darkness or upon a homogenous field (luminance = 0.47 cd/m^2) that subtended 5.35° horizontally and 1.36° vertically. The point targets were set to be 1 log unit more intense than the lighted rectangular background field. The two points were separated by a distance determined psychophysically to be the minimal perceptual gap. This proved to be 4.7′ for both subjects. The points and lighted background were generated on separate oscilloscopes (*Tektronix* 604, P4 phosphor) and combined by means of a beam-slitter.

A tracking trial, which lasted 40 sec, was initiated by the subject while he tracked the target whose motion was triangular along the horizontal meridian (peak-to-peak amplitude = 3.48°). Target velocity was either 141′/sec or 321′/sec and the subject (EK or RS) began each trial when he felt that his performance was as good as it could be.

Conditions were run as a 2 × 2 × 2 repeated-measures design in which each subject was tested against all possible combinations of velocity, target type, and background.

The analog output of the contact lens optical lever was digitized and analyzed by computer. Smooth pursuit gain (eye velocity/target velocity) was calculated to within 0.5% for each horizontal sweep of the target during the time the eye was near the center of the range of target motion. Sweeps in which saccades occurred were eliminated from the analysis. Details of the procedures used for data analysis are described elsewhere (Murphy, 1978). Murphy's

Table 1. Mean overall smooth pursuit gain for subjects EK and RS for each target velocity, background, and target type

	EK Gain	N	RS Gain	N
Velocity				
141′/sec	0.99 (0.11)	82	0.99 (0.05)	54
321′/sec	0.94 (0.13)	218	0.95 (0.09)	63
Background				
Dark	0.95 (0.12)	145	0.97 (0.08)	60
Light	0.95 (0.14)	155	0.96 (0.07)	57
Target type				
1 Point	0.93 (0.14)	138	0.97 (0.08)	61
2 Points	0.97 (0.12)	162	0.97 (0.08)	56

Standard deviations are given in parentheses and the number of tracks (*N*) for each condition is also shown.

experiment provided the extensive smooth pursuit practice which made the present experiment practicable.

RESULTS

Neither background nor target type influenced smooth pursuit gain. Mean overall smooth pursuit gains and their standard deviations for each velocity, background, and target type are summarized in Table 1. Note that gains on the lighted background were not higher than gains observed on a dark background. The 2-point acuity target did increase gain (4%) but for only one subject (EK). The other subjects's gains were the same for both types of target. Both subjects, however, did show an effect of target velocity on smooth pursuit gain (4–5%). Both showed higher gains with the lower velocity target.

The failure of background and target type to influence smooth pursuit gain, as well as the effect of target velocity, was confirmed by an analysis of variance which is summarized in Table 2. Only target velocity produced a statistically reliable effect on gain—background and target type did not. This was true for both subjects. None of the interactions of subjects and stimulus conditions showed statistically reliable effects.

The only reliable stimulus effect (target velocity) is illustrated by the histograms plotted in Figs 1 and 2. The main features of these graphs are that for both subjects tracking the lower target velocity the modal gain is 1.00 and the mediam gain is 1.01. At the higher target velocity EK's modal gain is lower (0.85) while

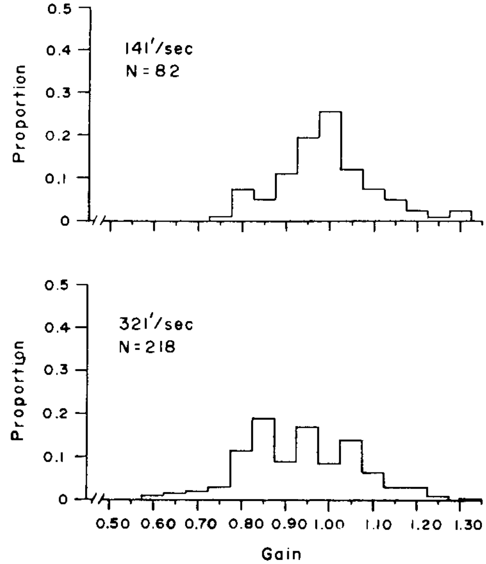

Fig. 1. Proportions of smooth pursuit gains for subject EK for the 141′/sec target velocity (top graph) and the 321′/sec velocity (bottom graph). The number (*N*) of tracks measured is also shown.

RS's modal gain is still 1.00. But note both subjects' median gains were still appreciably less than 1.00 with the faster target (RS median = 0.93, EK = 0.97). (See Table 1 for mean gains.)

We conclude that the subjects matched velocity (1.00 ± 0.005) with the slower target but not with the faster target. This conclusion can be supported by a statistical comparison of the distribution of low and high velocity gains with a hypothetical distribution whose mean gain equals 1.00. The hypothesis that the mean gain equals 1.00 could be rejected statistically for the higher target velocity (for RS, $t = 4.55$,

Table 2. Summary of the analyses of variance of smooth pursuit gain

Source	df	MS[a]	F
Velocity	1	9.5506	11.86*
Background	1	0.0766	0.95
Target	1	0.6126	0.76
Subjects	1	0.1626	0.20
Error[b]	11		

[a]Mean squares have been multiplied by 1000.
[b]The error term is based on the pooled sums of squares for all of the interactions terms. This error term was appropriate because none of the interactions was significant.
*$P < 0.01$.

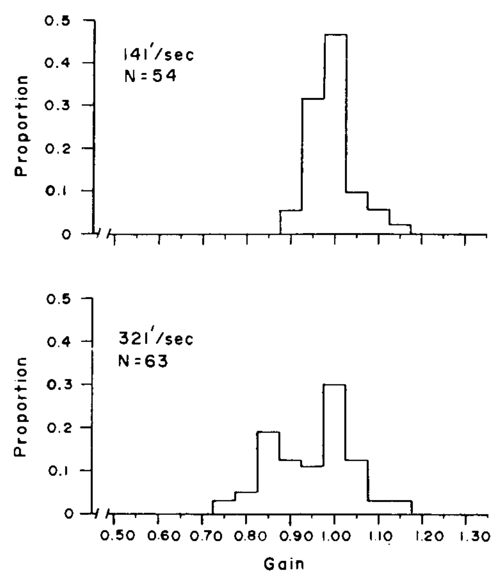

Fig. 2. Proportion of smooth pursuit gains for subject RS for the 141′/sec target velocity (top graph) and the 321′/sec target velocity (bottom graph). The number (*N*) of tracks measured is also shown.

$P < 0.0005$; for EK, $t = 7.33$, $P < 0.0005$) but could not be rejected for the lower target velocity (for RS, $t = 1.47$, $P > 0.05$; for EK, $t = 0.96$, $P > 0.05$).

DISCUSSION

Our finding that smooth pursuit gain was not influenced by the type of target or background upon which the target moved is not surprising because this finding is consistent with other research which shows that much larger variations of stimulus parameters, having large effects on visual perception, have negligible effects on oculomotor control (Steinman, 1965; Boyce, 1967; Rattle, 1969; Murphy, Haddad and Steinman, 1974; Murphy, Kowler and Steinman, 1975; Steinman, 1976; Winterson, 1977). We also found that an acuity target does not lead to higher gain than a single point. This finding leads us to believe that the fast foveal velocity-matching smooth pursuit subsystem proposed by Robinson (1976) is difficult to activate or, perhaps, not present.

We also found that maximum average gain of smooth pursuit can be 1.00 under some circumstances. This result implies that the smooth pursuit subsystem can "remember" target velocity. But, the ability of our subjects' smooth pursuit subsystem to perform in this manner was limited in at least two ways. First, it could only match velocity with a slowly moving target (2.4°/sec). There was appreciable retinal image slip (4–5%) with the higher velocity target (5.4°/sec). Note that our higher velocity is considerably below the velocity at which the human smooth pursuit subsystem is known to saturate (e.g. Westheimer, 1954, suggests about 30°/sec and Robinson, 1965, about 20°/sec).

Second, our subjects could only match velocity after considerable practice. This was evident in the performance of subject EK who had never previously attempted smooth pursuit before Murphy's (1978) experiment. During the first week of tracking practice, her mean gain with the 2.4°/sec target velocity was 0.82. During almost daily practice for a month her mean gain gradually and systematically rose to 0.99 (not distinguishable statistically from 1.00). Similar improvement occurred during practice with the 5.4°/sec target where mean gain started at 0.70 in the first week of practice and rose to 0.94. Such relatively slow and appreciable improvements in smooth pursuit (21% and 34%) suggest that velocity matching does not arise from the automatic operation of prewired neural circuits that "remember" target velocity. (See Murphy, 1978, for details of the practice and systematic changes in performance.)

There are additional possible limitations on the conditions under which eye velocity can match target velocity. First, can velocity matching be accomplished with unpredictable ramp displacements? If so, over what distance must the target travel before average gain equals one? Second, can velocity matching be accomplished with targets moving faster than 2.4°/sec? If so, what is the relative importance of the extent of target travel and the amount of practice to achieving such performance? Third, do practice effects on smooth pursuit gain generalize? We learned to match velocity with a target moving at 2.4°/sec. Does this also mean that we can match velocity with targets moving more slowly? We cannot answer any of these questions and conclude that human smooth pursuit is not yet completely understood.

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