Psychol. Belg. 1981, XXI-2, 93-110.

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PHI PHENOMENON, SMOOTH PURSUIT EYE MOVEMENTS AND VELOCITY SENSITIVE VISUAL MECHANISM

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Tracking eye movements are recorded in response to sequences of static stimuli appearing at various spatial and temporal intervals. The eye pursuit mean velocity is varying with the velocity simulated by the sequential static stimulation. Moreover, for a constant simulated velocity, the eye pursuit mean velocity varies with the spatiotemporal stimulation frequency. Therefore, some velocity sensitive motion detecting system is probably involved in the phi phenomenon as well as in the real motion perception. This mechanism will be more or less activated according to the spatio-temporal stimulation frequency.

INTRODUCTION

The phi phenomenon is the apparent motion (AM) produced by a sequential static stimulation (sss), i.e. by presenting a stationary visual stimulus in close successive locations. In an attempt to frame it within a matrix theory of vision, Saucer (1954) postulated separate functions for real or apparent motion perception on the one hand, and for form or detail perception on the other. Recent experiments have shown that the perception of motion and the perception of moving or stationary objects are effectively mediated by relatively distinct systems (see e.g. Tolhurst (1973) and Sekuler and Levinson (1977)). Therefore, it seems theoretically inadequate to take as a criterion of perception of phi phenomenon the continuity of perception of an apparently moving object. Moreover, such a methodological approach does not take into account the existence of the phi motion described by Wertheimer (1912) as an AM without any concomitant perception of a moving object, nor the possibility of perceiving an AM while detecting the discontinuity of the sss (Kolers, 1972a; Decostre-Voisin, 1973, 1977). These difficulties may account for the countless theories proposing one or another process by which a discontinuous stimulation

We are deeply indebted to Professor G. Thinès for his valuable help and advice. We would like to thank F. Huybrechts-Ameels and M. Roucoux-Hanus for subjecting themselves to the experiment, and C. Veraart for lending his visual stimulator. We are also grateful to C. Klepper, F. Langhendries-Vrins, S. Sarah, C. Hendrick, J. Schouppe and C. Stoquart for their kind assistance.

could give an impression of continuity, but not explaining the motion percept itself.

Studies of Clatworthy and Frisby (1973) in the psychological field and those of Grüsser-Cornehls, Grüsser and Bullock (1963), Barlow and Levick (1965), Michael (1966, 1968), Montero and Brugge (1969), Meulders, Godfraind and Veraart (1971) and Veraart, Meulders and Godfraind (1972) in the neurophysiological field, suggest that the perception of real motion (RM) and phi phenomenon could be mediated by the same mechanisms. However, Kolers (1963, 1964, 1972a, b; see also Kolers and von Grünau, 1976), has never accepted this proposal, on the basis of some differences between RM and AM. He emphasized (1963, 1964) that such a thesis does not account for the fact that a target, briefly flashed in the path of a really moving object, is harder to see the closer the two stimuli are, whereas the masking effect of an apparently moving object does not similarly vary with its apparent position relative to the target. In our opinion, this objection can be rejected out of hand, since there is no definite proof that any motion analysing system is involved in this masking phenomenon. Also, the latter can be explained by the laws of visual masking established for static stimuli. As stated by Kolers (1964), the nearer in time and space the masking stimulus is presented with respect to the target, the more difficult it is to see this target. The AM is not a stimulus, but a perception, and it may not obscure the fact that, in the above observation, the masking stimulus was physically closer to the masked one during the RM than during the AM condition.

According to Kolers (1964) one can observe a really moving object for a very long time without ceasing to perceive its motion, but if two alternate static stimuli are observed for the same period of time, all the parameters being held constant, an apparently moving object and two static flickering objects are perceived in turn. Such lability however is not always observed in the phi phenomenon: Thinès and Destercke (1971) hypothesized that the astonishing variability of the results obtained with two stimuli was due to excessively restrictive experimental conditions. Presenting many successive static stimuli along a virtual path, they observed that their numerous subjects reported seeing motion with an unusual regularity.

Another argument of Kolers (1963, 1972a) is that the path of an apparently moving object curves into depth 1. when the object is presented alternately in two locations, the interstimulus-interval being different from the intercycle-interval, 2. when a supra-threshold stimulus is placed as an obstacle along its potentially linear path or 3. when stimuli are spatially arranged in such a way that two apparently moving objects should phenomenally occupy the same place at the same time. A really moving object, on the other hand, does not undergo such a phenomenal path modification in similar conditions. However, preliminary observations of the authors suggest that apparently moving objects could also hold on their linear crossing paths when the apparently moving objects would occupy the same place at the same time,

provided the paths were marked by a sufficient number of stimulus locations.

Finally, according to Kolers (1964), the phi phenomenon would only occur at simulated velocities[1] ranging from 15 to 25 deg/sec, whereas the RM is perceptible at velocities ranging from 0.5 to 125 deg/sec, which would seem to imply that different mechanisms are involved. However, a number of authors have shown that the phi phenomenon can be elicited by means of sss simulating velocities approaching the lower threshold of RM perception (Biederman-Thorson, Thorson and Lange, 1971; Banks and Kane, 1972; Destercke, 1973, 1974; Decostre-Voisin, 1973). On the other hand, many authors such as Wertheimer (1912), Neuhaus (1930, in Kolers, 1972a) and Kahneman (1967), have studied AM by presenting a single stimulus in only two successive locations. Under such conditions, the phenomenal simultaneity predominated and the upper threshold of AM was underrated. AM and phenomenal simultaneity are indeed widely compatible when the stimulus is presented in more numerous successive locations (Allport, 1968; Decostre-Voisin, 1973). It is well known that the maximum velocity at which RM can be perceived increases with the path length (Smith, 1969a); similarly, the larger the number of successive locations, the higher the upper threshold of AM.

The upper threshold of real and apparent motion have been compared more in detail elsewhere (Decostre-Voisin, 1977). It has been hypothesized from the works of Smith (1969 a, b), Allport (1968, 1970), Biederman-Thorson et al. (1971), Efron and Lee (1971) and Decostre-Voisin (1973), that the upper threshold of real as well as apparent motion perception is related to the visual persistence of the stimulus, which varies itself with the stimulus brightness and with some parameters of the RM or of the sss, as e.g. velocity or distance between successive locations. The threshold would correspond to some motion or sss duration just lower than the duration of perception of the stimulus as a form in its initial location. This would imply that some velocity-signal may be "post-cancelled" by some more persisting information about form localization.

This proposition needs to be investigated in detail, but the available evidence seems to indicate that threshold differences, if any, between real and apparent motion could be related to stimulation disparity rather than to some differences in underlying mechanism.

According to some authors, some mechanisms involved in RM perception and in phi phenomenon are identical. MacKay (1958, 1961)[2] observed that if an object — some parts of which are self luminous — is illuminated with a stroboscope — e.g. at 6 Hz —, and if the image of the object is moved faintly over the retina by pressing lightly the

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[1] The velocity simulated by a sss is given by the quotient of the inter-stimulus distance by the onset to onset delay separating the successive stimuli.

[2] In McKay, 1973.

canthus of the eye (the other being closed), only the steadily lit parts of the object seem to be moving; conversely, when the object is moved about, the observing eye remaining still, the same lit parts apparently float free of the object, until its movement has ceased (MacKay, 1958)[3]. In order to explain these peculiar phenomena, MacKay (1973) hypothesized that two mechanisms are involved in motion perception: one sensitive to change in position and the other sensitive to the continuous drift of the retinal image, coding velocity as such. According to MacKay, the visual system is more sensitive to some RM than to any AM of the same amplitude because the first activates both mechanisms of motion detection while a sss only influences the position sensitive mechanism. The perceived amplitude of motion would depend on the joint action of both mechanisms, which would explain in turn the phenomena described above.

Biederman-Thorson et al. (1971) for their part, are claiming that the phi phenomenon is mediated by the same mechanism as RM perception when the distance between stimuli is relatively short, but that it could depend on another process when the stimuli are widely spaced.

Finally Braddick (1974) theorized that the mechanism mediating phi phenomenon differed according to whether the distance between stimuli was greater or less than 20 min of arc.

The aim of the present study is to investigate whether an sss can activate some velocity sensitive motion detecting system, especially when the spatial or temporal stimulation frequency is low. It seemed to us that a good indication of the activation of such a system could be found in eye movement. Indeed, it is well known that eye pursuit velocity varies with target velocity (Dodge, Travis and Fox, 1930; Westheimer, 1954; Rashbass, 1961; Robinson, 1965; Dichgans, Nauck and Wolpert, 1971). This amounts to saying that some velocity sensitive mechanism is involved in the eye pursuit velocity control. It is therefore hypothesized that a sss may activate the above mentioned velocity sensitive mechanism, provided that pursuit eye movements are recorded during stimulation and that the pursuit velocity varies with stimulus simulated velocity.

METHOD

The electronic stimulator used was designed by Veraart (1970a, 1974) for the analysis of single units visual receptive fields. It consisted of a black and white TV-picture tube, the screen of which was 0.65 m in diagonal; the usual TV flicker effect was excluded and the electroluminescent layer of the screen had a retentivity of less than 0.2 msec. The stimulus was a luminous spot subtending a visual angle of 3 min of arc relative to an observer sitting 1 m away. Its brightness was 1.1 Cd/m^2. Figure 1 shows schematically the different stimulation

[3] In Gregory, 1964.

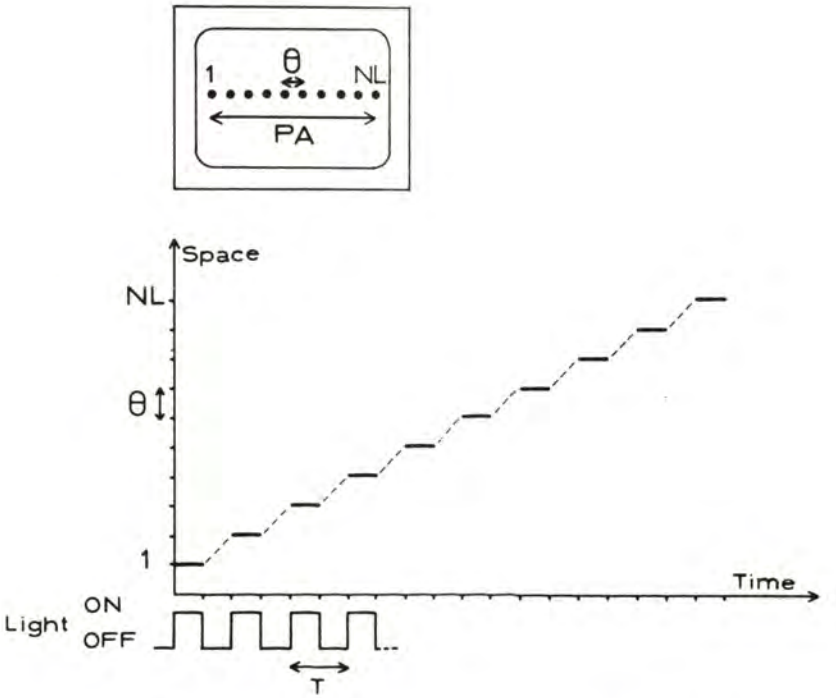

FIG. 1. DIAGRAM OF STIMULATION. See text for explanations.

parameters: The spot was successively presented in a number, NL, of locations along a horizontal; θ was the distance in visual angle between two successive locations; T was the period, i.e. the time interval between two successive onsets; PA was the path length, i.e. the distance between the first and last stimulus locations; the spot was presented in each location for half a period and was turned off during any change of position. Stimulation conditions are shown in Table 1, which illustrates how velocities of 3, 6, 12, 24 and 48 deg/sec were simulated for various distances and periods between stimuli. It is to be noted that the resulting visual impressions were spatially and temporally fused, i.e. stimulation discontinuity was not perceived, only when short distances and periods were used (Decostre-Voisin, 1973). To each distance (θ) was associated a number (NL) of successive stimulus locations, these values determining together the length PA of the path. The 23 combinations of parameters (θ) and (T) were presented in random order, 8 times to subject FA and 4 times to subject MR, the stimuli being displayed successively at random either from left to right or from right to left. The stimuli were composed outside the subject's view, on a control desk equipped with a control screen and with a switch allowing for disconnection of the stimulation screen during the setting.

TAB. 1. STIMULATION CONDITIONS. θ, distance between stimulus successive locations (min of arc); T, period or onset to onset interval (msec); NL, number of stimulus successive locations; PA, length of the virtual path (deg of arc); the simulated velocity (deg/sec) is given by the relation θ/T.

NL	90	90	70	40	20	10
PA	7,4	14,8	23	26	25,3	24
θ	5	10	20	40	80	160
T	simulated velocities					
14	6	12	24	48		
28	3	6	12	24	48	
55		3	6	12	24	48
110			3	6	12	24
220				3	6	12
440					3	6

Horizontal eye movements were monitored as follows: The subject sat in a dark room with his head in a headrest; sharply focused rays of infra-red light were projected on his left eye; two photodiodes were aimed at the iris-sclera boundary on each side of the staring eye; next, each of these cells caught varying amounts of reflected infra-red light, depending on whether the eye, while turning, presented to one or the other a greater proportion of sclera or iris; the difference between the two photocurrents, providing a measure of the eye position, was amplified and then recorded on magnetic tape; eye movements to the right (left) were so converted into positive (negative) voltages.

The two subjects were unaware of the purpose of the experiment and both had normal sight. The experiments were conducted over a number of sessions of some 40 minutes, each with integrated rest periods, and were spread over several months. At the initial session the subject was told that luminous dots would appear on the screen in sequence and was instructed to focus his eyes on each dot as soon as possible. Before each sss he was told to fixate the middle of the screen until the first dot appeared. Tracking eye movements were recorded from the first dot onset on (NL + 1).T milliseconds.

After each adjustment of the photocells, a target was presented successively in 10 locations which were spread on a row, symmetrical to the center of the screen, and 160 min of arc apart from each other; the subject was instructed to fixate the target in its actual location and 400 msec later the output voltage from the eye monitor system was recorded during 250 msec for calibration purpose.

All recordings were processed off-line by a PDP-12 system as follows: the analog-digital conversion of the eye monitor system output was made at a 400 Hz frequency, under the control of the program Catacal (DEC-12-UW1A-D). Resulting data, except those relating to calibration, were submitted to the Catacal smoothing operation before being stored

on magnetic tape. Eye velocity computing and further analysis of the recorded movements were programmed in Focal-RT (Decus-Program Library n° 12-80) (Decostre-Voisin, 1977): A saccade was detected when the eyeball had reached a mean velocity of 31 deg/sec during 12.5 msec; the saccade was then delimited with an accuracy of 2.5 msec, the criterion being an eye velocity higher than 30 deg/sec[4]. The remainder of the recording was then divided into parts 20 msec long which were parcelled out, on the basis of the mean eye velocity during this time, among the following categories: 1. smooth eye movements to the right (eye velocity higher than 2 deg/sec), 2. smooth eye movements to the left (eye velocity lower than —2 deg/sec) and 3. fixation. The mean velocity of the smooth eye movements executed in the direction in which the static stimuli succeeded one another was then computed. Finally, the results so obtained were averaged for each combination of 0 and T values.

RESULTS

Figure 2 presents the mean eye pursuit velocity as a function of the target simulated velocity, the period (T) being taken as a parameter. It may be seen that regardless of the duration of the period, the mean eye pursuit velocity increases with the simulated velocity as long as the latter does not exceed 24 deg/sec. Paradoxically, the mean pursuit velocity decreases as the simulated velocity rises from 24 to 48 deg/sec; this is probably due to the brevity of the corresponding sss (574 to 605 msec) together with the increase in eye pursuit latency which takes place when some target moves suddenly in one direction, then uniformly and rapidly in the opposite direction (Robinson, 1965) (Fig. 3). Therefore, these three conditions in which the stimulus velocity equals 48 deg/sec were ignored in computing the correlation between the mean eye pursuit velocity and the simulated velocity. Table 2 shows that for the 20 remaining conditions the Spearman rank correlation coefficient reaches .88 in subject FA and .70 in subject MR, those values being significant at level .005 (one-tailed test). If one considers only the conditions in which 0 is greater than or equal to 20 min of arc, i.e. the conditions allowing the perception of the stimulation discontinuity in space, one finds a Spearman rank correlation coefficient of .90 (.67) in the subject FA (MR), significant at the .005 level. Further, the correlation coefficient between the mean eye pursuit velocity and the simulated velocity remains significant at the .005 level if one takes only into account the conditions in which the period is 220 or 440 msec, i.e. when the stimulation discontinuity in time is evident. Finally, Table 2 shows the Spearman rank correlation coefficient between mean eye pursuit velocity and simulated velocity, obtained for the greatest values of 0 and T in our experiments; it should be noted that in subject MR the

[4] It was very unlikely that the smooth pursuit exceeds 30 deg/sec in our experiment, since the stimulus virtual path was rather short.

TAB. 2. CORRELATION BETWEEN SMOOTH PURSUIT MEAN VELOCITY AND SIMULATED VELOCITY. r_s, Spearman rank correlation coefficient; p, significance level (one-tailed test); θ, distance between successive stimuli (min of arc); T, period (msec). The three 48 deg/sec conditions are excluded from the computation. See text for further explanations.

CONDITIONS		Sbj FA		Sbj MR	
θ	T	r_s	p	r_s	p
5 → 160	14 → 440	.88	< .005	.70	< .005
20 → 160	14 → 440	.90	< .005	.67	< .005
20 → 160	220 → 440	.68	< .005	.72	< .005
160	110 → 440	.94	< .005	.50	< .05
80	55 → 440			.76	< .01
80 → 160	440	.43	< .05	.60	< .05
40 → 160	220	.75	< .005	.79	< .005

TAB. 3. CORRELATION BETWEEN SMOOTH PURSUIT MEAN VELOCITY AND DISTANCE (θ) OR PERIOD (T), AT CONSTANT SIMULATED VELOCITY. r_s, Spearman rank correlation coefficient; p, significance level (one-tailed test); SV, simulated velocity (deg/sec).

SUBJECTS	FA		MR	
SV	r_s	p	r_s	p
6	—.53	< .005	—.56	< .005
12	—.67	< .005	—.50	< .025
24	—.61	< .005	—.90	< .005

correlation is significant at a level less than .01 when θ equals 80 min of arc, and at a level less than .005 when T equals 220 msec; in subject FA, the Spearman coefficient is significant at levels less than .005 and 0.5 respectively when θ equals 160 min of arc and when T equals 440 msec.

Figure 4 shows that the mean eye pursuit velocity decreases when longer and longer distances (θ) are used to simulate some constant velocity. Obviously a similar graph could have been plotted with period (T) in abscissa. Table 3 gives the Spearman rank correlation coefficient between the mean eye pursuit velocity and the distance (θ) or the period (T), the simulated velocity being held constant. This correlation is rarely very high[5], but negative in all cases; it is highly significant for simulated velocities of 6, 12 and 24 deg/sec[6].

[5] The relation between the pursuit velocity and the distance (θ) may be slightly masked, as a longer path is more favourable to an adequate pursuit in the case of AM (Decostre-Voisin, 1977) as well as of RM (Dichgans et al., 1971) and as the length (PA) of the path was rather longer when θ was larger (see Table 1).

[6] The data collected for simulated velocities of 3 and 48 deg/sec cannot be interpreted in this connection: at 3 deg/sec the eye pursuit hardly emerged of the noise level and, on the other hand, the simulated velocity of 48 deg/sec only led to an obviously inadequate pursuit (see Fig. 2 and 3).

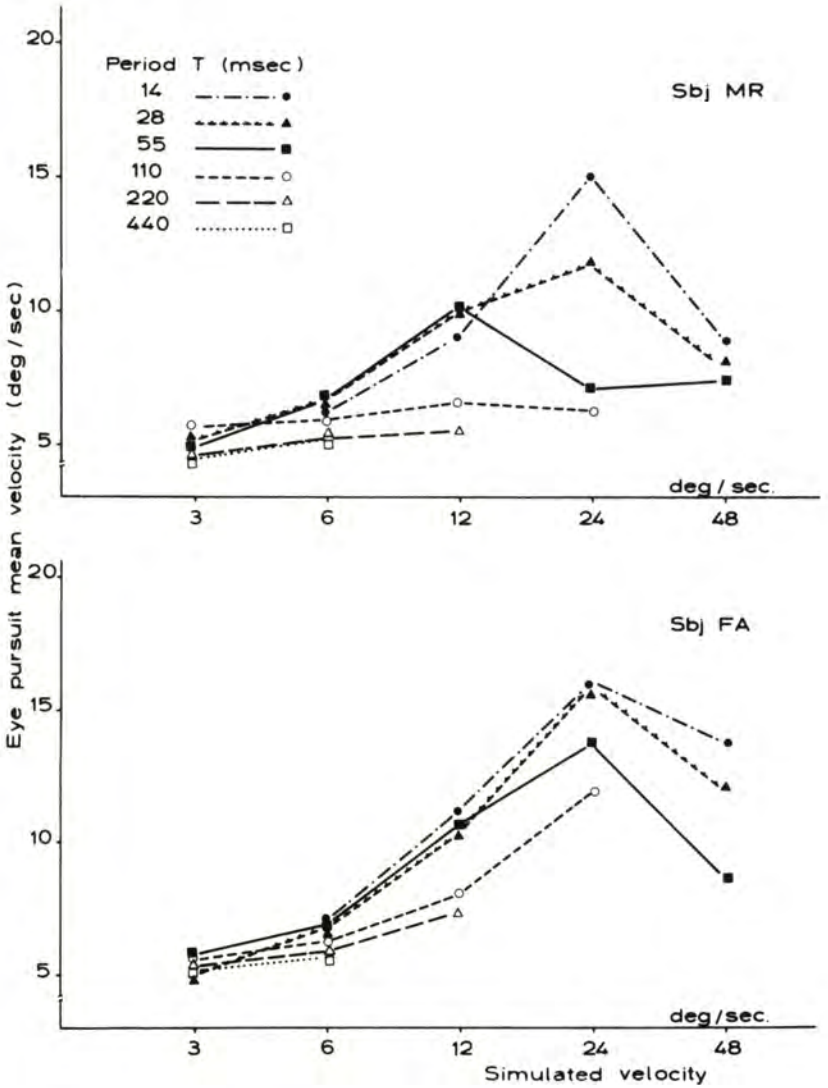

FIG. 2. EYE PURSUIT MEAN VELOCITY AS A FUNCTION OF STIMULUS SIMULATED VELOCITY, ACCORDING TO PERIOD (T).

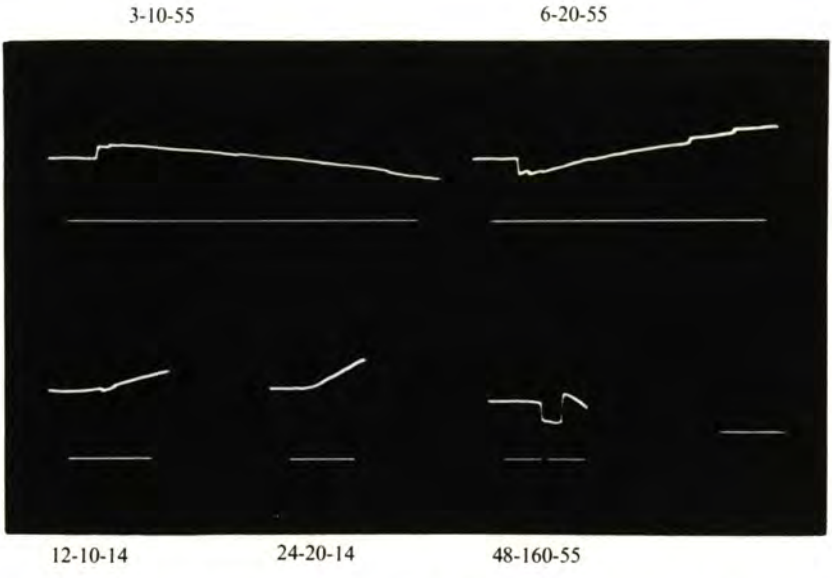

FIG. 3. EYE MOVEMENT RECORDS IN SUBJECT MR. Rightwards eye movements upwards; the lower trace shows the sss duration; the numbers indicate for each tracing and from left to right, the simulated velocity (deg/sec), the distance, θ (min of arc) and the period, T, (msec); calibration: horizontal, 1 sec. It should be observed that for the simulated velocity of 48 deg/sec, the smooth pursuit is hardly begun during the first sss, but becomes obvious if the stimulation is repeated at a short interval; however, the eye movements were quantitatively analyzed during the first sss only.

DISCUSSION

The two subjects actually executed smooth pursuit eye movements in response to sss simulating velocities ranging from 3 to 48 deg/sec; successive stimuli were from 5 to 160 min of arc apart from each other and onset to onset intervals ranged from 14 to 440 msec. The rather wide range of possible variation of these parameters contrasts strongly with the minimum input for the smooth pursuit control system as defined by Daley (1972), who ascertained that a smooth pursuit eye movement of 80 msec minimum was executed in 50 per cent of the trials when distance and time between static stimuli were respectively 1 deg of arc and 50 msec, which simulated a velocity of 20 deg/sec. The difference may possibly be ascribed to the fact that he took into account only the eye movements recorded between 100 and 400 msec after the beginning of the sss.

SIMULATED VELOCITY

The significant correlation of the pursuit eye movement mean velocity

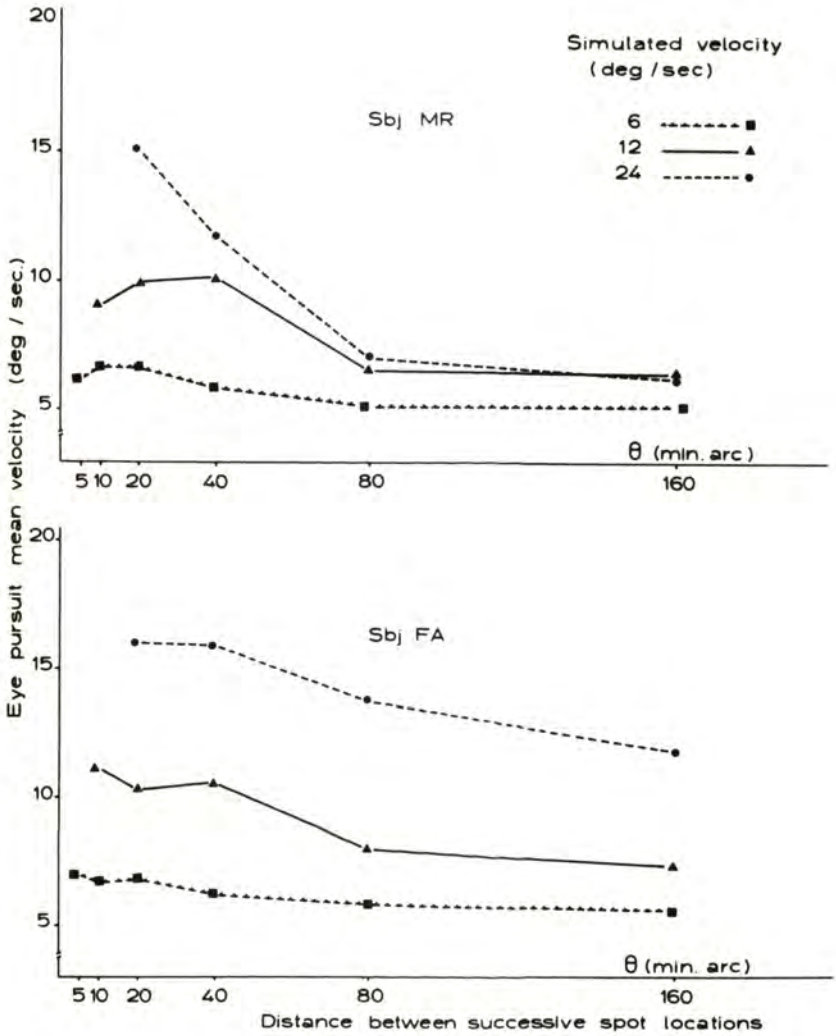

FIG. 4. EYE PURSUIT MEAN VELOCITY AS A FUNCTION OF DISTANCE (θ), ACCORDING TO STIMULUS SIMULATED VELOCITY.

with the stimulus simulated velocity shows that in the case of sss as well as in that of a RM (Dodge et al., 1930; Westheimer, 1954; Rashbass, 1961; Robinson, 1965; Dichgans et al., 1971), the smooth pursuit is controlled by some motion detecting mechanism which codes velocity. This amounts to saying that some velocity sensitive system can be activated not only by a "continuous" sweep on the retina but also by static stimuli sequentially projected on non-adjacent receptors.

This does not fit with MacKay's theory (1973), according to which only some position sensitive motion detecting system would be implied by phi phenomenon, the velocity sensitive system requiring a continuous drift of some image on the retina to be activated. It is consistent however with the fact that a motion after effect can be produced by means of iterative sss (Anstis and Moulden, 1970; Banks and Kane, 1972)[7]. Indeed, any motion after effect in one direction is generally ascribed to some temporary inhibition of visual motion sensitive neurons having their "preferred" direction at 180 degrees relative to that of the after effect (Barlow and Hill, 1963). These neurons must belong to a system dealing with velocity rather than with displacement, since there is no displacement perception in this after effect (Gregory, 1964, 1966; Bonnet, 1971). Moreover, Banks and Kane ascertained that the duration and the phenomenal strength of the movement after effect increased with the stimulus simulated velocity.

Finally, observing that smooth pursuit eye movements could be recorded during some sss when AM was reported, Young and Chu (1975) concluded that smooth pursuit was controlled by perceived movement rather than by retinal image motion. Since a sss can activate the same motion detecting system as a "continuous" sweep on the retina, Heywood's (1973) observations seem to support more convincingly the perceptual feedback hypothesis than the observations of Young and Chu. The latter are nevertheless of great interest: similarly to ter Braak's (1972) results, they suggest that pursuit eye movements during sss are accompanied by a conscious perception of motion, although the pursuit is not a necessary condition of the phi phenomenon (ter Braak, 1972)[8].

Further, it has been noted that the correlation between the pursuit mean velocity and the simulated velocity remained highly significant ($p = .005$, one tailed test) in both subjects when the stimuli were displayed 20 min of arc or more apart from each other or when the period reached 220 or 440 msec. This would mean that the velocity sensitive mechanism involved can be activated by a sss having a relatively low spatial or temporal frequency, consequently perceived as flickering. Moreover, the adaptation of the eye velocity to the

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[7] Kolers (1972a) raised as an objection to the identity of the mechanisms involved in RM and AM perception the fact that the AM produced by two successive stimuli did not elicit a movement after effect (Humphrey and Springbett, 1946).

[8] It seems nevertheless that smooth pursuit eye movements can raise considerably the upper threshold of AM perception together with the threshold of phenomenal simultaneity (Decostre-Voisin, 1977); it may also be taught that these movements are favourable to the fusion of successive separate stimuli into a continuous perception of only one object. Lastly, if smooth pursuit eye movements are executed in front of a stationary periodic pattern which is illuminated stroboscopically, they can elicit an apparent motion perception of the pattern (Lamontagne, 1973; Heywood, 1973; see also Grüsser, Pause and Schreiter, 1979), perhaps because in such conditions the corollary discharge (Teuber, 1960) is hardly cancelled by reafferent information. In the case of a sss however, the corollary discharge may be more or less cancelled according to the value of the ratio stimulus duration/period.

simulated velocity indicates that the simulated velocity has been perceived. Since this adaptation still occurred when the sequential stimulation appeared to be flickering, it may be said, as Kolers (1972a) and Decostre-Voisin (1973) suggested, that a movement can not only be inferred but also actually perceived without any continuous perception of a moving object.

It might be objected that from the outset, smooth pursuit eye movements — or eventually foveation movements (Hallett and Lightstone, 1974) — reduce the distance between successive stimuli at the retinal level and that it is therefore doubtful that the mechanism involved is dealing with stimuli as distant from each other. As a matter of fact, the actual distance, θ_r (in visual angle), between consecutively stimulated retinal loci is the difference between simulated velocity and ocular velocity, multiplied by the period (in seconds). If for each combination of distance (θ) and period (τ), θ_r is estimated for the mean velocity of pursuit shown in Fig. 2, numerous values greater than 20 min of arc are found: In subject FA e.g., when $\theta = 160$ min of arc, $\theta_r = 130$, 81 and 62 min of arc respectively for $\tau = 55$, 110 and 220 msec; in subject MR, when $\theta = 80$ min of arc, $\theta_r = 67$, 56 and 36 min of arc respectively for $\tau = 28$, 55 and 110 msec. As the correlation between pursuit velocity and simulated velocity is still significant at level .005 (.01) in subject FA (MR) when $\theta = 160$ (80) min of arc, it provides evidence for the activity of the velocity sensitive system in these conditions, challenging Braddick's (1974) hypothesis that different processes are involved in AM perception according to whether the distance between stimuli is shorter or longer than 20 min of arc.

Neurophysiological studies of Barlow and Levick (1965) and Michael (1968) dealing with retinal ganglion cells of the Rabbit and the Ground Squirrel, led to the belief that lateral interaction processes accounting for the directional selectivity in movement sensitive neurons would be at work only on distances shorter than 0.5 deg of arc. Montero and Brugge (1969) have found however in lateral geniculate body of the Rat some directionally selective unit which was strongly activated or inhibited by a sequence of static stimuli 2.5 deg of arc apart from each other, according to whether the sequence progressed in its "preferred" or in the opposite direction. A related observation was made by Meulders et al. (1971; see also Veraart et al., 1972) at the pulvinar level in the Cat, with successive stimuli separated by a distance up to 6 deg of arc. This suggests that the phi phenomenon could possibly be demonstrated objectively for distances between stimuli longer than those used in our experiments, provided a large number of successive stimuli is presented.

Regarding the temporal interval between stimuli, Veraart (1970b, 1976) recorded in the lateral geniculate body and in the posterior and lateralis posterior thalamic nuclei of the Cat. The evoked activity of single units showed that processes of lateral interaction were at work when static stimuli were presented at some distance from each other

and at an interval as long as 800 msec or even 2 sec. It remains to be proved however, that such long time interactions indeed play a part in the sensitivity of neurons to motion. From the psychological point of view, Zeeman and Roelofs (1953) claimed that an optimal motion could still be perceived when the period reached 2.5 sec, but the phi phenomenon was not objectively demonstrated in such conditions.

STIMULATION FREQUENCY

Since a velocity sensitive motion detecting system can be activated by a sss as well as by a RM, it would seem that the additional information supplied by a continuous movement as compared to a sss is redundant. This however is not the case since we ascertained that for a constant simulated velocity, the eye pursuit mean velocity decreased with the spatio-temporal frequency of stimulation. Moreover, according to Banks and Kane (1972) the perceived speed of the AM also decreases with the spatio-temporal stimulation frequency. Thus it would seem that the eye pursuit velocity varies in conjunction with the perceived speed of the tracked AM and that the velocity sensitive mechanism involved underestimates the target simulated velocity the more the stimulation frequency is lowered[9].

Electrophysiological studies by Godfraind, Meulders and Veraart (1969, 1972), Meulders et al. (1971) and Veraart et al. (1972) suggest that in the Cat, non primary nuclei of the postero-lateral thalamus could play a part in complex visual functions related to motion perception. In particular, Veraart (1970b) noticed an increase of the instantaneous discharge rate of a motion sensitive unit in the pulvinar, related to an increase in the stimulus velocity. More recently Orban (1975) observed that in area 18 of the Cat, the evoked response of many neurons increased as the stimulus velocity was increased. In this connection, the fact that the perceived speed of AM decreases with the stimulation frequency would mean that the velocity sensitive mechanism is less activated as the spatio-temporal frequency of stimulation is lowered.

Veraart's work (1976; see also Decostre-Voisin, Meulders and Veraart, 1975) gives some support to this view. This author recorded in the thalamic postero-lateral nucleus a single unit which reacted strongly and with the same directional selectivity to RM and to various sss, though it was unresponsive to any isolated static stimulus. When the stimulation was in the preferred direction at a nearly constant simulated velocity of about 12 deg/sec, the mean discharge rate increased with the spatio-temporal stimulation frequency, approximating asymptotically the response level obtained for a RM of the same velocity.

The above hypothesis could account for the fact noted by Kolers

[9] It should be interesting to compare experimentally pursuit velocity during sss and during RM, the stimulus (simulated) velocity and all other stimulation parameters being kept constant. This experiment was attempted but unfortunately invalidated by a defect in path amplitude control in the RM mode.

(1964) that the velocity of a RM has to be lower than the simulated velocity of any AM in order to obtain the same apparent speed. It would give an account of the impossibility of catching a flying projectile in intermittent light, noted by Croft (1971), the speed of the object being probably underrated in such conditions. It would also account for the fact noticed by Banks and Kane (1972) that the duration and the phenomenal strength of a movement aftereffect increase with the spatio-temporal frequency of the inducing iterative sss, the simulated velocity of which is left unchanged. Moreover, the fact noted by MacKay (1973), that the visual system seems to be much more sensitive to a continuous motion of the image over the retina than to a discontinuous displacement through the same visual angle, could be understood that way. Finally, to account for the perceptive dissociation which can occur between continuously and discontinuously illuminated portions of a moving object (MacKay, 1958, in Gregory, 1964), it may be hypothesized that an amplitude signalling mechanism is serially connected to the velocity sensitive system, as Orban (1975) suggested from his neurophysiological data.

According to the last hypothesis, the more the simulated velocity is underrated, the more the target is perceived lagging behind the position it would occupy at any time if it was in RM at that velocity. Morgan and Turnbull (1978) presented separately to the two eyes of their observers two identical targets in AM, simulating the same velocity; an interocular delay in presentation of the targets to corresponding retinal positions resulted in a depth shift of the binocularly fused target. These authors claimed that a "virtual disparity" eliciting the depth effect arised from the AM of the first target during the delay, but they did not explain satisfactorily why this effect progressively broke down when the interval between successive target exposures was increased by steps, from 50 to 200 msec. Keeping in mind that in such conditions the simulated velocity is more and more underrated as it decreases, one may believe that finally the "virtual disparity" reached no longer the stereo-acuity threshold.

Lastly, it has been noted that the smooth eye pursuit of an apparently moving object was interrupted by an increasing number of saccades as the temporal frequency of the sss decreased (Decostre-Voisin, Meulders and Veraart, 1973; Morgan and Turnbull, 1978). In these conditions, the simulated velocity becomes more and more underrated and the smooth pursuit less and less adequate with respect to the target successive physical positions. At the onset of the target in any location on its path during the tracking, the resulting fixation error would become available for the visuo-oculomotor system and if required, a saccadic correction would be triggered.

In conclusion, the above discussed phenomena seem to indicate that the same velocity sensitive mechanism may be involved in the AM and RM perception and in the smooth pursuit control.

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Received November 1980