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Different Programming Modes of Human Saccadic Eye Movements as a Function of Stimulus Eccentricity: Indications of a Functional Subdivision of the Visual Field

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Abstract. 1. Voluntary saccadic eye movements were made toward flashes of light on the horizontal meridian, whose duration and distance from the point of fixation were varied; eye movements were measured using d.c.-electrooculography.—2. Targets within 10°–15° eccentricity are usually reached by one saccadic eye movement. When the eyes turn toward targets of more than 10°–15° eccentricity, the first saccadic eye movement falls short of the target by an angle usually not exceeding 10°. The presence of the image of the target off the fovea (visual error signal) subsequent to such an undershoot elicits, after a short interval, corrective saccades (usually one) which place the image of the target on the fovea. In the absence of a visual error signal, the probability of occurrence of corrective saccades is low, but it increases with greater target eccentricities. These observations suggest that there are different, eccentricity-dependent modes of programming saccadic eye movements.—3. Saccadic eye movements appear to be programmed in retinal coordinates. This conclusion is based on the observations that, irrespective of the initial position of the eyes in the orbit, a) there are different programming modes for eye movements to targets within and beyond 10°–15° from the fixation point, and b) the maximum velocity of saccadic eye movements is always reached at 25° to 30° target eccentricity.—4. Distributions of latency and intersaccadic interval (ISI) are frequently multimodal, with a separation between modes of 30 to 40 msec. These observations suggest that saccadic eye movements are produced by mechanisms which, at a frequency of 30 Hz, process visual information.—5. Corrective saccades may occur after extremely short intervals (30 to 60 msec) regardless of whether or not a visual error signal is present; the eyes may not even come to a complete stop during these very short intersaccadic intervals. It is suggested that these corrective saccades are triggered by errors in the programming of the initial saccadic eye movements, and not by a visual error signal.—6. The exitence of different, eccentricity-dependent programming modes of saccadic eye movements, is further supported by anatomical, physiological, psychophysical, and neuropathological observations that suggest a dissociation of visual functions dependent on retinal eccentricity. Saccadic eye movements to targets more eccentric than 10°–15° appear to be executed by a mechanism involving the superior colliculus (perhaps independent of the visual cortex), whereas saccadic eye movements to less eccentric targets appear to depend on a mechanism involving the geniculo-cortical pathway (perhaps in collaboration with the superior colliculus).

Introduction

Stimuli which appear in the periphery of the visual field and which attract our attention are foveated by saccadic eye movements (SEMs). Only one SEM occurs for stimuli close to the visual axis; targets with great eccentricities are acquired by two or even more SEMs (Becker and Fuchs, 1969; Frost and Pöppel, 1974). We attempted to study systematically the properties of SEMs as a function of stimulus eccentricity.

Methods

1. Experimental Paradigm

Three adult subjects without visual or oculomotor pathology participated in these experiments. A Tübinger perimeter (Sloan, 1971) was used for the presentation of targets. Subjects viewed the dome monocularly through their natural pupil; the unused eye was covered with a patch. The subject's chin rested on a platform so that his eye was centered in a half spherical dome of 33 cm radius. The subject's head faced the middle of the dome which formed a homogeneous white field with a luminance of 3.18 cd/m^2 (low photopic range). Both the fixation point and the spots toward which subjects were to move their eyes were presented along the horizontal meridian of the dome. The subject fixated either in primary position (head and eyes are oriented in the same direction), or eccentrically, i.e. the fixation point was laterally displaced, and SEMs were in the direction towards primary position. Visual targets consisted of stationary white spots 10' arc in diameter and with a luminance of 31.8 cd/m^2. Targets were projected at increments of 5° distance from the fixation point. No targets were presented in the temporal field between 10° and 20° eccentricity because of the blind spot in that region. At each position, targets were presented for a short duration (always 100 msec) and a long duration (which was constant in a given experiment but varied from 2.0 to 4.3 seconds between experiments). In each experiment, the duration and location of the target presentations were varied independently according to pseudo-random schedules.

Prior to each experiment, subjects were adapted to the luminance of the perimetric hemisphere. They knew in advance that targets would be presented only along the horizontal meridian, and in a given experiment only the nasal or the temporal visual field was tested. No warning was given prior to the presentation of a target. Subjects were instructed to stare at the fixation point until a target appeared, at which time they were to move their eyes as quickly as possible to the position of the target, fixate there for about 1 s, and then move their eyes back to the fixation point. In the case of 100 ms flashes, the target disappears before the subjects are able to move their eyes towards the target, because the latency of SEMs is approximately 200 ms (Robinson, 1964); this stimulus situation is referred to as the "open loop" condition. Whenever these short-lasting targets occurred, subjects were instructed to move their eyes to the point where the flash had appeared. Subjects were specifically directed never to move their heads, and an observer standing in back of them made certain that this instruction was strictly obeyed. Great care was taken not to fatigue the subjects. During an experiment, targets were presented at intervals of approximately 5–10 s, and no more than 16 targets were presented consecutively (in one run) without a rest break of a few minutes. The mean latency and the mean peak velocity of the subjects' SEMs did not show any tendency to change systematically over the duration of the experimental sessions, indicating that the preceding procedures were effective in preventing fatigue.

2. *Eye Movement Recording and Calibration*

Eye movements were recorded using dc-electrooculography (EOG). The subject's skin was thoroughly cleaned using acetone, and silver-silver chloride skin electrodes were placed at the outer canthus of each eye with a reference electrode in the center of the forehead. The electrodes were allowed to stabilize for approximately one hour before the experiment began. Signals from the electrodes were amplified by a dc-amplifier and displayed on a strip chart recorder. A stimulus maker recorded the presentation of a target. The frequency response of the recording system was adequate to insure negligible distortion of the signal from the electrodes. Preliminary experiments with 5 other subjects indicated that great attention must be paid to accurate calibration and to the linearity of the recording system over the range of ocular deviations to be measured. It was found that calibration could change significantly from run to run and showed minor fluctuations over the course of a single run. Calibration curves became non-linear for ocular deviations greater than approximately 30° either side of primary position. In recognition of these difficulties, the following calibration procedure was adopted. Within each run, at each position tested, at least one target was presented in the "closed loop" condition (target presentation for 2 or more seconds), allowing the subject to accurately foveate the targets before returning his eyes to the fixation point. The random distribution of such long-lasting targets throughout each individual run assured that small random fluctuations in gain over the course of the run were cancelled out in the best fit calibration line relating pen deviation to the eccentricity of the targets. Changes in calibration due to long-term changes in the EOG signal, or slight differences in head position from run to run, were corrected since each run was calibrated only by SEMs made during the 2–3 min duration of that run. When eccentric fixation was employed (up to 20°), calibrations were linear over the entire range of eye movements tested (up to 45°). When in a given run, calibration points up to 30° from primary position were not well-fit by a straight line, the data from that run were not used.

In these experiments it was important to insure that all subjects were actually able to turn their eyes toward all of the targets presented. Subjects can not report accurately for very eccentric fixations whether or not they are looking towards a target. Therefore, a better method has to be used than simply asking the subjects whether they are fixating. After an experiment, the subjects were told to fixate a small bright spot in primary position for approximately 10 s. This fixation established a foveal after-image. The subject was then asked to superimpose this afterimage on small spots of light of increasing eccentricity until he could no longer do so. The eccentricity of the last spot for which the subject can perform the required superimposition is a precise measure of the maximum ocular deviation. All subjects could easily deviate their eyes beyond 40° from primary position. Thus, when a subject fixated a point 20° to one side of primary position, we were certain that he could accurately execute SEMs up to 45° in amplitude toward the opposite side of primary position, and that such eye movements would fall within the linear range of the recording system.

3. *Data Processing*

The amplitudes of pen deviations, latencies, and intersaccadic intervals were measured by hand. With the gains and paper speeds used, amplitude resolution was approximately 0.5 degrees of arc, and temporal resolution was approximately 5 ms. Straight lines were fit to calibration points "by eye" and the slopes calculated. The peak velocity of a SEM was measured by the angle between the baseline and a line drawn tangent to the SEM at its steepest point. The pen deviation, the paper speed, and the calibration slopes were then used to derive the appropriate scalings.

Results

1. *Latency and Intersaccadic Interval*

For both conditions of target presentation (100 msec: open loop; 2.0 to 4.3 sec: closed loop) the latency of SEMs was measured as a function of the target distance from the fixation point. Under closed loop conditions one often observes a second SEM (or "corrective saccade") after the first one, and the interval between the end of the first and the beginning of the second SEM (henceforth referred to as intersaccadic interval or ISI) has also been measured as a function of target eccentricity. Results of one typical experiment are illustrated in Fig. 1. The data show that neither the latency nor the intersaccadic interval vary systematically as a function of target eccentricity. Sometimes, however, there are small decreases in latency as eccentricity increases from 5° to 10° and in some experiments (especially with one subject, RD) latency was observed to increase for targets beyond 35° eccentricity. These changes are small compared to the variability of the latency at each target eccentricity, and they are not statistically significant. For example, in one experiment, the

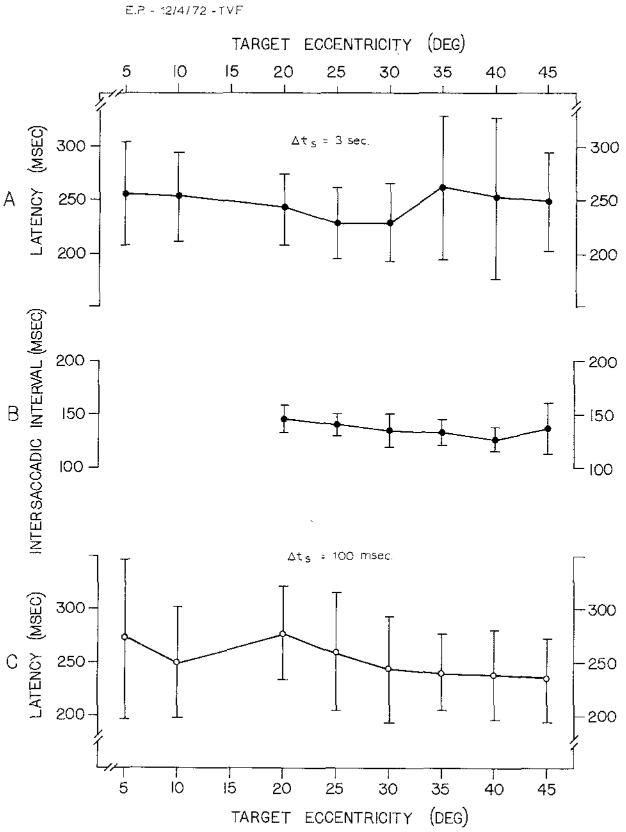

Fig. 1. An example of latency and intersaccadic interval of SEMs as a function of the distance of the target from the fixation point. (A) Latency of the first SEM for target presentation time (Δt_s) of 3 s. (B) Interval between the end of the first and the onset of the second SEM for Δt_s of 3 s. (C) Latency of the first SEM for Δt_s of 100 ms. Targets are presented in the temporal visual field (TVF). Fixation point is 20° nasal of primary position. Vertical lines: Standard deviation

latency to targets close to the visual axis was as follows (mean ± standard deviation): 2°: 250 ± 55 msec; 4°: 244 ± 41 msec; 6°: 233 ± 41 msec. Analyses of variance also failed to show any significant differences in the latencies of SEMs to targets presented under open- and closed loop conditions.

The data presented in Fig. 1 show another typical feature of SEMs observed in these experiments, i.e. a conspicuous difference in the duration and variability of the latency and the intersaccadic interval; the latency of the first SEM to an eccentric target is greater and has a much greater variability than the ISI. The differences between the latency of the first SEM, and the intersaccadic interval, with respect to duration and variability, suggest some essential difference in the programming mode of these two movements.

As there was no systematic dependence of latency and of ISI on target eccentricity, histograms indicating the likelihood of occurrence of particular values of these parameters at any eccentricity may be produced, using all of the data of one experiment, irrespective of target position. In Fig. 2, a few histograms are shown as examples. It is striking that the majority of these histograms is multimodal. A histogram is considered as multimodal using the following convention: take the maximum of a given histogram as the reference point; draw a horizontal line at 50% of this reference point; if there is more than one peak above this line, the histogram is considered to be multimodal; if there is only one peak above this line, the histogram is considered to be unimodal. Thus, only the histogram of Fig. 2d is unimodal. The interval between the peaks in the multimodal histograms was, in most cases, 30 to 40 msec.

Under the conditions of these experiments, the average latency and the average intersaccadic interval were approximately 250 msec and 140 msec, respectively. One subject (SC) sometimes showed much shorter ISIs; they were occasionally as short as 30 msec, as is indicated in Fig. 2e. An original record illustrating one such short ISI (approximately 50 msec) is shown in Fig. 3. The eyes do not come to a complete stop during this intersaccadic interval. The corrective saccade which occurs after this short ISI is followed by a second corrective saccade; however, the ISI between these SEMs is longer than 200 msec. Such rather long intersaccadic intervals are usually seen under open loop conditions, i.e. when the visual target is no longer present.

It has been shown (Becker, 1972) that the duration of intersaccadic intervals is negatively correlated with the magnitude of the subsequent corrective saccades. This same negative correlation was observed in the experiments reported here and the earlier observations can thus be confirmed.

2. *Magnitude of the First SEM*

In Fig. 4 the magnitude of the first SEM as a function of stimulus eccentricity is illustrated for a typical experiment. The magnitudes of first SEMs are similar, regardless of whether the target is presented in the open- (100 ms) or closed-loop (3 s) condition. The first SEM very rarely overshoots the target.

Independent of flash duration and of the fixation condition (primary position or eccentric fixation), targets presented within 10°–15° of the visual axis elicit one SEM of sufficient amplitude to align the visual axis with the target. Visual targets presented beyond 10°–15° eccentricity elicit SEMs that are usually too short to reach the target. The inset of Figure 4 shows that both in the open- and closed-loop conditions the first SEM undershoots the targets beyond 10°–15° eccentricity. In practically all cases the undershoot increases rapidly as target eccentricity increases beyond

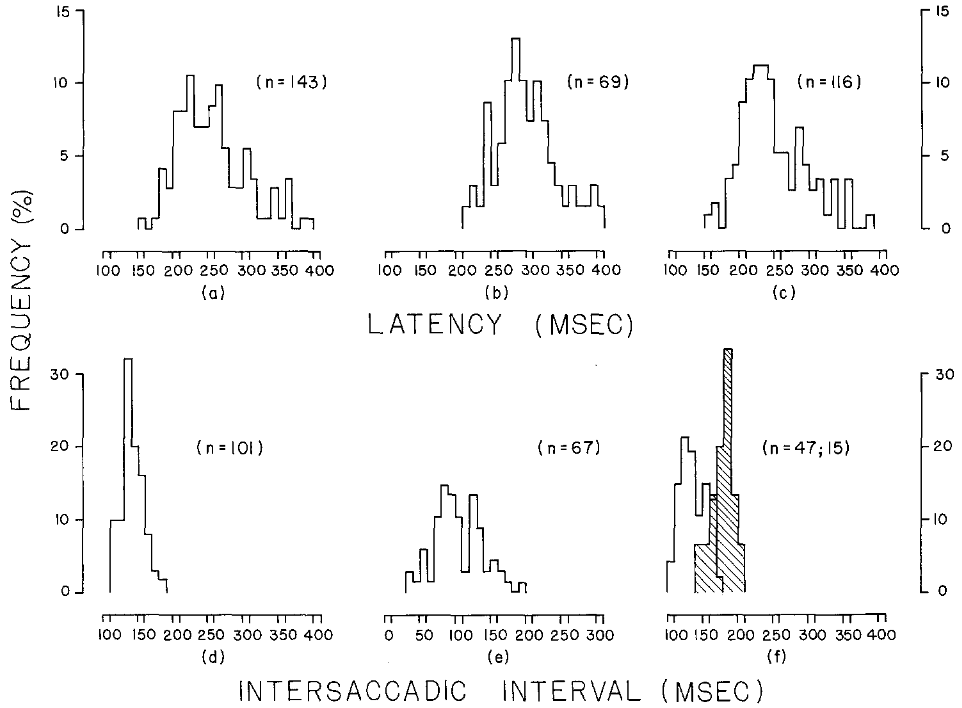

Fig. 2. Examples of normalized histograms of latency of SEMs (top row) and of intersaccadic interval (bottom row). For (a), (b), (c), and shaded distribution in (f), Δt_s is 100 ms; for (d), (e), and unshaded distribution in (f), Δt_s is 3 s. Targets are presented in the temporal visual field except in (c). Fixation conditions: (b) primary position; (a), (d), and (e) 20° nasal of primary position; (c) 20° temporal of primary position; (f) 5° nasal of primary position. Data from (a) and (d) are from the same experiment with subject EP; (c) and (f) are separate experiments with EP; (b) subject RD; (e) subject SC

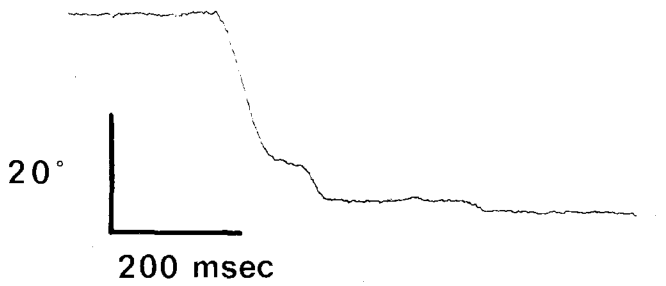

Fig. 3. Original record of a SEM of subject SC. Δt_s is 100 ms (see stimulus artifacts); the target is presented in the temporal visual field, fixation is 20° nasal of primary position

10°–15°. The increase in the undershoot may level off or it may increase up to the most peripheral target positions (as in Fig. 4). Because SEMs to targets beyond 10°–15° eccentricity usually undershoot the true target position, corrective saccades are necessary in order to obtain foveation of these more peripheral targets.

3. *Probability of Corrective Saccades*

The probability of a visual target eliciting more than one SEM is a function of both the position of the target in the visual field and the duration of its presentation. Figure 5 summarizes the results of two typical experiments. In the closed loop condition, the probability of eliciting more than one saccade is very low (zero, in most cases) up to 10° target eccentricity, whereas for more peripheral positions the probability of occurrence of corrective saccades increases rapidly and then levels off at a very high value (often 100%).

Under open loop conditions, all subjects made only one saccade toward targets at eccentricities of 10° or less. Responses to a 100 msec flash more peripheral than 10° vary from subject to subject and in the same subject at different times. Figure 5 shows that in one experiment, subject EP made corrective saccades only to targets at 45° eccentricity when tested in the open loop condition, while during another experiment, 100 ms flashes of increasing eccentricity had an increasing likelihood of eliciting more than one corrective saccade. Subject SC, when tested in her temporal visual field, also had an increasing probability of making a corrective saccade toward more peripheral 100 ms flashes, but she made corrective saccades much more frequently than EP. It is important to stress that under closed loop conditions the probability of more than one SEM is also always very low for targets at 5° and 10° eccentricity, irrespective of the initial position of the eyes in the orbit.

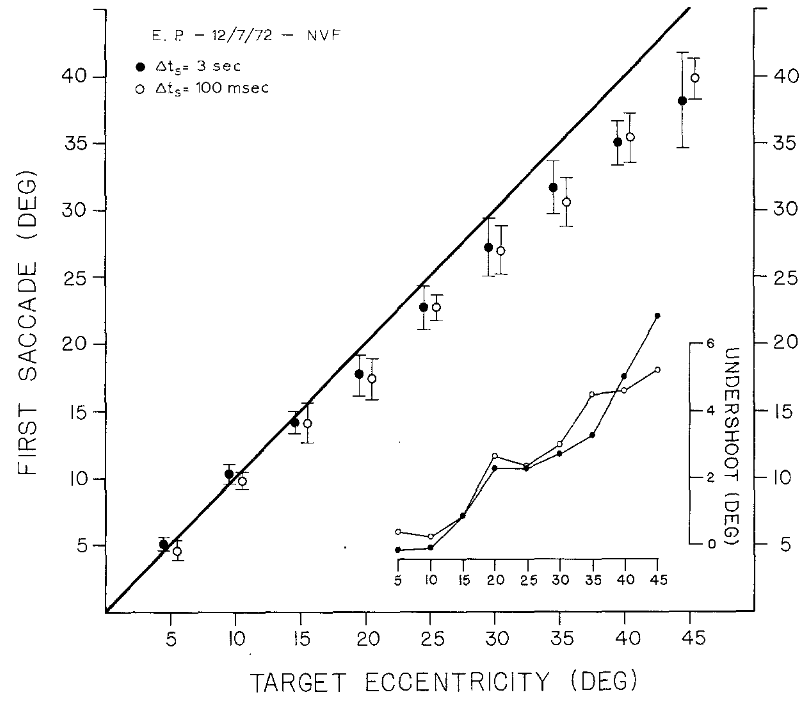

Fig. 4. Magnitude of the first SEM as a function of target eccentricity. Inset in lower right shows mean amount by which first SEM falls short of target, as a function of target position. Targets in this experiment were presented in the nasal visual field (NVF), fixation was 20° temporal of primary position. Vertical lines: Standard deviation

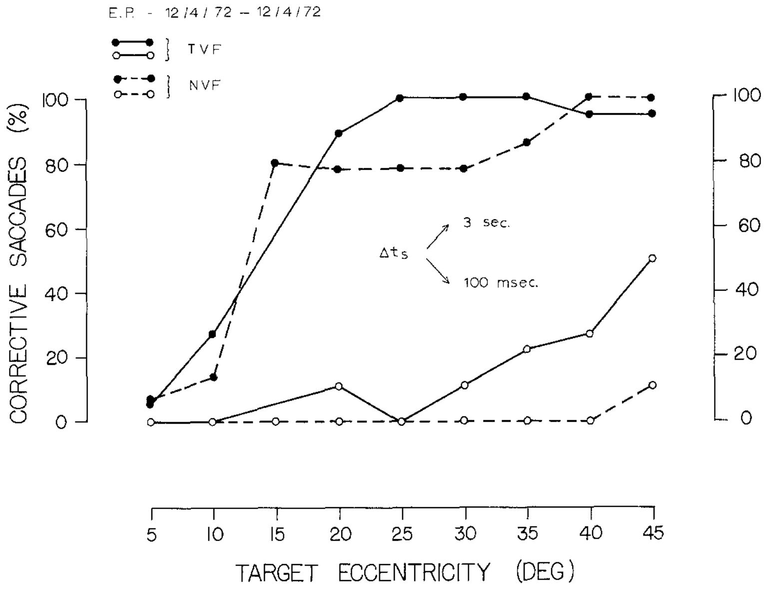

Fig. 5. Probability of one or more corrective saccades subsequent to the initial SEM, as a function of target eccentricity. Upper two curves are for Δt_s of 3 s, lower two curves are for Δt_s of 100 ms. Solid lines indicate target in temporal visual field (TVF), fixation was 20° nasal of primary position. Broken lines indicate target in nasal visual field (NVF), fixation was 20° temporal of primary position

4. Velocity of SEMs

The peak velocity of the first SEM is determined by the eccentricity of the target. The relationship between peak velocity and target eccentricity during two typical experiments is shown in Figure 6. The illustration shows that, for a given initial position of the eyes in the orbit, peak velocity of the first SEM is the same under open- and closed-loop conditions. Irrespective of the starting position of the eye, the maximum velocity increases with increasing eccentricity for targets located up to 25°–30° from the point of fixation; for more peripheral targets velocity remains roughly constant with a value approximately the same as that measured at 30° eccentricity. For a given target eccentricity, the maximum velocity of SEMs varies with the initial position of the eyes in the orbit (Fig. 6). With eccentric fixation and SEMs towards primary position and beyond it, peak velocity is higher than with fixation closer to the primary position of the eyes in the orbit.

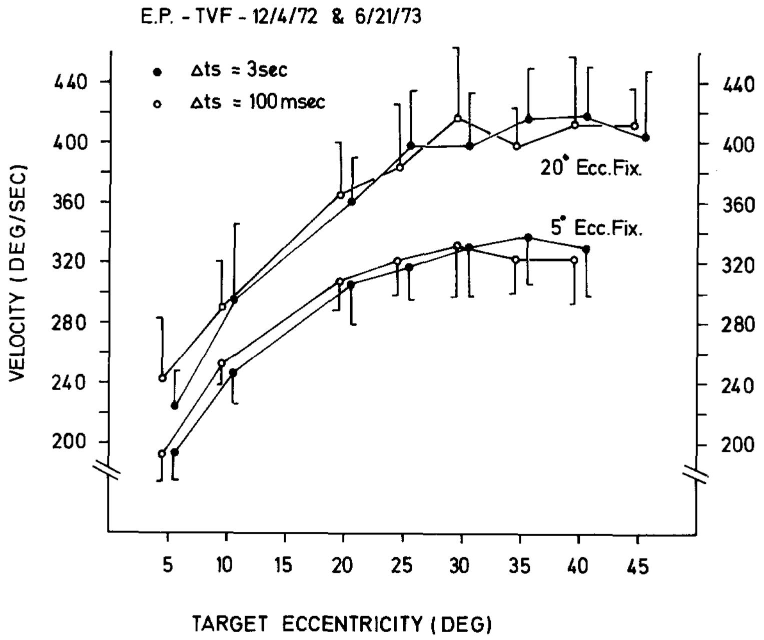

Fig. 6. Peak velocity of the first SEM as a function of target position in temporal visual field (TVF) with different starting positions of the eye in the orbit (5° and 20° nasal of primary position). Targets are presented under open-($\Delta t_s = 100$ ms) and closed-loop ($\Delta t_s = 3$ s) conditions

Discussion

1. Multiple Programming Modes of Saccadic Eye Movements

We observed that the latency, magnitude, and peak velocity of the first SEM toward visual targets of a given eccentricity are independent of the duration of the target presentation (100 msec and 2 to 4.3 sec), and that a longer presentation time prior to the first SEM does not improve its accuracy or precision.

Targets up to 5°–10° eccentricity are foveated by one SEM; at greater eccentricities the first SEM consistently falls short of the target regardless of the presentation time, and a corrective saccade is necessary to bring the target onto the visual axis. Thus, there appears to be a qualitative difference in the modes of programming SEMs to targets nearer and farther than a 10°–15° critical distance from the visual axis. While the critical eccentricity for a change in the strategy of foveation appears to be approximately 10°–15°, increments in target position of 5° are too great to allow a more accurate determination.

The possibility that the oculomotor system "preprograms" two SEMs in response to targets of greater eccentricity has already been suggested by Becker and Fuchs (1969). Perhaps positional information adequate to accurately align the target with the visual axis is not available to the oculomotor system unless the target is within 10°–15° of the fixation point. Becker (1972) has also reported that overshoots by the first SEM are infrequent; he pointed out that "by making undershoot the general rule perhaps the decision as to whether the corrections should be positive or negative is economized" (p. 238). More specifically, we propose three reasons that programming the first SEM *to fall short* of targets with great eccentricity may represent the most efficient strategy for directing the gaze toward the target (if for whatever reason such targets cannot be reached by one SEM). First, the distance between the target and the fovea (retinal error) after completion of the first SEM will be computed on the same side of the brain, because the target remains in the same visual half-field; the computation might be easier and faster if the other side of the brain is not involved at any time in the determination of retinal error. Second, if the first SEM falls short, the corrective saccade will always go in the same direction as the first SEM, and a decision whether the corrective saccade is to the left or to the right is not necessary. Perhaps this reason is related to the fact that the intersaccadic interval under closed loop conditions is much shorter than the latency of the first SEM (140 vs. 250 msec). Finally, less muscular energy is required in this strategy.

One should expect a third programming mode for SEMs to targets which, due to their eccentricity, are foveated by combined eye and head movements. We can not describe this mode in greater detail since our experiments were performed with the head fixed. Behavioral observations of Bartz (1966) and physiological studies by Bizzi et al. (1972) suggest specific strategies of eye and head coordination for the foveation of very eccentric targets.

2. Correction of Programming Errors

Most corrective saccades seem to conform to the preceding description in that they appear to be preprogrammed to occur following the execution of the first SEM to targets more eccentric than 10°–15°. The intersaccadic interval in these instances is usually not less than 100 ms and, in the closed loop condition, the magnitude of the corrective saccade is determined by the visual error signal present after the completion of the first SEM.

In both the open- and closed-loop conditions, one subject (SC) occasionally executed corrective saccades which we believe to be a distinct population because of the extremely short (30–60 ms) intersaccadic intervals preceding them. They usually occur when the undershoot of the first SEM is extremely large. The data of Becker (1972) also include a few such very brief ISIs. During these ISIs, the eyes sometimes do not come to rest, as they do during longer intervals (see Fig. 3). As 85 msec appears to be the minimal possible latency for visually controlled corrective saccades (Robinson, 1973), it is suggested that corrective saccades preceded by a much shorter intersaccadic interval are programmed independent of visual information from the retina. We propose that there may be a mechamism internal to the central nervous system which compares the programmed magnitude of the first SEM and the stored retinal error signal; if the programmed undershoot of the eye movement is too great, this mechanism may elicit another SEM without awaiting the arrival of a visual error signal. This hypothesis implies that corrective saccades preceded by a very short intersaccadic interval differ from other corrective saccades in that they are not preprogrammed, but rather, are elicited in an attempt to compensate for a programming error. The internal signal representing the programmed SEM magnitude might be an "efference copy" signal of the sort proposed by von Holst and Mittelstaedt (1950) in their discussion of the apparent stability of the visual world. Alternatively, a programming error may be indicated by proprioceptive input from the extraocular muscles, which with very short latency reaches parts of the cerebellum which participate in the control of eye movements (Fuchs & Kornhuber, 1969).

3. *Sampling of the Visual Input*

It was observed that most histograms of latency and intersaccadic interval are multimodal (see Fig. 2). What appears to be significant in connection with the results of others is the fact that the distance between the modes was 30 to 40 msec. In a report by Fuchs (1967, Fig. 6) histograms of latency are shown, which are based on larger samples; at least three modes are clearly visible in each histogram and the intermodal distance is in all cases 30–40 ms. Similar multimodal histograms for choice reaction time to visual stimuli have been reported by Pöppel (1970). It is interesting to note that a periodicity of approximately 30 Hz (30–40 ms period length) has been observed in several studies on temporal processing (e.g., Augenstine, 1955; Latour, 1967).

The simplest way to interpret multimodal histograms with regularly spaced modes is to assume underlying periodic processes. Whenever a target appears, or one saccade is completed, it would seem that an oscillatory process with a frequency close to 30 Hz is entrained or triggered within the central nervous system. The periodicity must be phase-locked to the presentation of the target (or to the completion of the first SEM): As has been discussed in the "paternoster" model by Pöppel (1970), if the periodicity had no fixed phase relationship to the presentation of the target, multimodal histograms could not occur. Assuming a continuously running oscillatory process, targets would appear at all phases because of the random intertrial intervals and the oscillation would not produce the multimodal histograms.

The 30 Hz frequency suggested by the multimodal histograms may indicate that visual input is sampled with such a frequency. Sampling mechanisms with a much lower frequency (approximately 5 Hz) have been suggested by Young and Stark (1963). Some observations of Wheeless et al. (1966) support the idea of a faster sampling mechanism. They reported that if a visual target undergoes two sudden displacements, for intervals between the displacements of up to 100 msec, SEMs may be directed toward the final target position rather than its intermediate position. Therefore, the position of the target must be sampled after the second target displacement, and this new information can override the programming of the SEM started by the first target displacement. Alternatively, visual information may be continuously available, while there is a periodicity in the initiation of eye movements by stations in the oculomotor system further removed from the visual input. Such an arrangement would make use of visual information only at regular intervals, and would be equivalent to a sampling of the visual input.

In Fig. 2f the histogram of intersaccadic interval in the closed loop condition shows peaks at 120 and 150 msec; the histogram in the open loop condition shows a peak at 180 msec. All three peaks are separated by intervals of 30 msec, as would be expected if there is an underlying stimulus-entrained or -triggered periodic process. These data suggest that the oculomotor control program may sample several times for a retinal error signal. The mean duration of the intersaccadic interval in the open loop condition is considerably longer than in the closed loop condition. In the absence of a retinal error signal, the oculomotor system may, after one or a few sampling intervals, release a corrective saccade, if the first SEM has been much too small. We have proposed above that the oculomotor system programs more than one SEM to turn the eyes toward targets of more than 10°–15° eccentricity. However, the notion that the visual input is sampled prior to the execution of a corrective saccade suggests that although the *occurrence* of that corrective saccade may be preprogrammed, its *magnitude* is not determined until after the execution of the preceding SEM and the measurement of the remaining retinal error over one or more 30–40 msec sampling intervals.

4. A Hypothesis Relating Structure to Different Programming Modes of SEMs

We have suggested that differences in the number of SEMs necessary to foveate targets nearer and farther than 10°–15° from the point of fixation indicate distinct modes of programming saccadic eye movements. A number of other morphological and functional observations support the notion that there are differences in the processing of visual information within and beyond the central 10°–15° of the visual field.

Van Buren (1963) observed that surrounding the foveal and perifoveal areas of the retina, there is a region whose central limit is about 10° and in which ganglion cell density remains constant at a value that is less than in more central zones. There is a similar plateau in the distribution of brightness increment threshold in the visual field. Pöppel and Harvey (1973) observed that contrast sensitivity decreases under photopic conditions and increases under scotopic conditions from the fovea up to approximately 10° eccentricity. Beyond 10°, one observes a plateau of constant sensitivity up to 35° eccentricity in the temporal visual field and up to 20° in the nasal field. The plateaus of ganglion cell density and contrast sensitivity start approximately at that eccentricity that is suggested as the critical distance for programming either one or two SEMs.

Hubel, *et al.* (1975) have recently demonstrated by autoradiographic tracing of retinofugal connections, that in the monkey, the organization of the retinal projection to the superior colliculus differs in the area of the tectum representing the central part of the visual field (approximately 15° either side of the vertical meridian as judged from their Fig. 2) and the region representing the more peripheral parts of the visual field. In the zone representing the central part of the visual field, the retino-collicular innervation is considerably less dense than in the remainder of the tectum, and the manner in which the terminal arbors of axons originating in the two eyes are segregated differs in the representations of the central and peripheral portions of the visual field. Previous studies had failed to demonstrate any direct central retinal projection to the superior colliculus (Wilson and Toyne, 1970; Lund, 1972; Bunt et al., 1974), although this had been challenged on physiological grounds (Schiller et al., 1974). The reason for these results might be that axons of the central retinal region differ qualitatively or quantitatively from axons of more peripheral retinal regions. It could well be that axons from the central retinal region are so thin, that they cannot be visualized by the histological techniques previously employed. Cowey (1974) has demonstrated that in monkeys subjected to long-term bilateral ablation of cortical area 17, there is heavy retrograde transneuronal loss of ganglion cells within 10°–15° of the fovea, while the density of ganglion cells peripheral to 15° is normal. The absence of sustaining projections to the superior colliculus among most of the ganglion cells of the central retina suggests that, both anatomically and physiologically, the central retina is more intimately related with the geniculo-striate system than with the superior colliculus. In the hamster, the telodendria of retino- and cortico-tectal axons are distributed through the thickness of the stratum griseum superficiale (SGS) in an approximately complimentary fashion; following ablation of either one of these two afferent systems in neonatal animals, the axonal arbors of the other proliferate and take over the space normally occupied by the one which is absent (Schneider, 1974; Gower & Schneider, unpublished). These data suggest that in the primate, the cortical projection to SGS may be more highly developed in that zone of the superior colliculus which represents the central visual field than it is in the remainder. We are currently investigating this possibility.

These observations also have correlates in pathology. Pöppel et al. (1975) described an eccentricity-specific effect on critical flicker fusion in patients with occipital lobe lesions. They showed that after a unilateral lesion, critical flicker fusion is diminished in the contralateral visual half-field at 5° eccentricity but not at 20° eccentricity. They also showed an increase in the latency of SEMs to 5° eccentric targets but not to 20° eccentric targets in the hemifield contralateral to the lesion. These results suggest that in humans there is a functional dissociation between the center and periphery of the retina which may reflect the differential organization of the retinocollicular input.

Studies of "residual vision" in patients with lesions of the central visual pathways (Pöppel et al., 1973; Weiskrantz et al., 1974) suggest that SEMs can be directly initiated by the superior colliculus. In these experiments visual targets were presented in areas of the visual field which were "blind" due to lesions of the visual cortex; these lesions leave the retino-collicular projection intact. It was shown that the location of targets presented within cortical scotomata is discriminated by SEMs, although the curve showing SEM amplitude as a function of target eccentricity had a slope of much less than one. This might be due to an imbalance of inhibition between the two superior colliculi, resulting from the cortical lesion (Sprague, 1966). Experiments in monkeys (Mohler and Wurtz, 1974) suggest that this capacity to discriminate visual targets is due to a collicular mechanism. Thus, the superior colliculus can inform the rest of the oculomotor system about the eccentricity of visual targets in the absence of the visual cortex.

On the basis of these observations and our own results, we would like to suggest the following hypothesis concerning two programming modes of SEMs. Whenever a target appears at up to 10°–15° eccentricity, the processing of positional information is dependent on the geniculo-cortical pathways; the retinal error is measured exactly and only one SEM is programmed by the oculomotor system, which presumably receives the retinal error information through a cortico-collicular pathway. Whenever a target appears beyond 10°–15° eccentricity, the positional information is transmitted directly from the retina to the superior colliculus. A first SEM is programmed by the oculomotor system on the basis of visual information represented in the superior colliculus. This first SEM is meant to quickly bring the visual axis close to the target, but it is programmed to fall short of the target. After completion of the first SEM, the remaining retinal error, which in this experiment is usually well below 10°, is measured with the participation of the geniculo-cortical system, and the corrective saccade is programmed on the basis of this measurement. The two modes of programming SEMs reflect, therefore, different modes of information processing in the central and peripheral zones of the visual field. Studies on visual and vestibular movement perception also suggest two eccentricity-dependent modes of information processing with approximately the same boundaries (Brandt et al., 1973). Finally, on the basis of teleological arguments, and the results of behavioral testing of split-brain monkeys, Trevarthen (1968) has suggested that vision involves two parallel processes; one "focal", which is restricted to the central visual field, "examines detail in small areas of space," and is mediated by the visual cortex; the other "ambient", "determining space at large around the body," and mediated by the superior colliculus.

Thus, the present results as well as the other structural and functional observations cited in this section, suggest that the visual field may be divided into central and peripheral zones for which important aspects of information analysis in the central nervous system are qualitatively different, and whose border lies 10°–15° from the point of fixation.

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