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SENSORIMOTOR TRANSFORMATION DURING EYE MOVEMENTS TO REMEMBERED VISUAL TARGETS

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Abstract—For eye movements made to visual targets, the brain must transform the retinotopic coordinate frame of the visual system to that of the oculomotor plant. Ideally, responses should exactly match target demands. However, during eye movements to remembered targets, responses are spatially distorted. The transformation does not retain accurate retinotopic registration, having both constant and variable components of error. Generally, the constant pattern of distortion appears as a hypermetria for upward saccades and a hypometria for downward movements. Most of the error accumulates during the first 800 msec of memory-contingent delay. The results are interpreted with respect to theories of how spatial information may be coded and transformed.

Saccades Sensorimotor Memory Macaque Human Spatial maps Eye movements

INTRODUCTION

Visual spatial information is gathered by the retina in a retinotopic coordinate frame in which spatial position is encoded as the relative positions of the receptors which are excited by the impinging light. To guide accurate motor behavior, the brain must transform this spatial information from the retinotopic coordinate system to that of the appropriate motor plant. Furthermore, despite that the eyes can move about within the orbits, we are quite capable of guiding eye and limb movements with a high degree of accuracy. The brain must account for these additional degrees of freedom. These issues were recognized long ago by a number of investigators (Helmholtz, 1910; Sperry, 1950; Von Holst, 1954), and it is generally accepted that perceptual and motor constancy is achieved in the brain by combining signals related to eye position with the retinotopic signals (Mays & Sparks, 1980a). Combination of these two signals produces information which is coded in a higher level egocentric frame of reference which, in the case of combination of eye and retinal location, would be called a craniotopic coordinate frame. Obviously, higher order combinations of head position relative to the body and other bodily relations are possible and even necessary for more complex motor control.

Additionally, it is possible to make eye movements to the remembered location of visual targets which have disappeared. Therefore, we must assume that the brain is able to hold some form of spatial representation of oculomotor targets which are not dependent on the physical presence of the target. Little is understood about where and in what form this neural representation might exist. It could exist in terms of retinotopic coordinates in visually-related neurons which do not require the physical presence of the stimulus; it could exist as motor coordinates in neurons coding planned movements; or it could exist in spatial coordinates independent of retinotopic or oculomotor parameters. Furthermore, these representations need not be mutually exclusive.

In this study we sought to gain some insight into the special case of sensorimotor coordinate transformation in which eye movements are made to remembered locations of visual targets. At a minimum, for the brain to solve this task it must transform retinotopic spatial information into a memory-linked spatial representation (of unknown coordinate frame) and eventually to the motor coordinate system representing change in eye position with respect to current eye position. We show here that eye

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movements to remembered targets differ from movements to visual targets in both their temporal and spatial parameters. These studies were performed on both humans and rhesus monkeys. Determining the similarity of responses for the two species allows for cross-correlation of the neurophysiological data which has been obtained from monkeys and the psychophysical and perceptual data obtained from humans.

The end position of eye movements made to remembered targets represents the output of the sensorimotor transformation from a retinotopic input to the oculomotor response, without the benefit of visual feedback to guide the movement or to correct for inaccuracies. If the transformation by the brain was perfect, the response would exactly match the input demand. Instead, we found the oculomotor responses were spatially distorted. Furthermore, this distortion was shown to be specific to the remembered target task, and therefore assumed to be a function of the memory dependent process inherent in the task. This distortion contained a constant and a variable component. The constant component varied somewhat between individuals, but in most subjects in included hypermetric movements for upward saccades and hypometric eye movements for downward saccades. This systematic distortion was of greater magnitude for the monkeys. Additional experiments investigated the contribution of eye and head position in an effort to gain insight into the coordinate frames of reference involved in the transformation process. The effects of training, task dependence and additional non-target visual information also were investigated. The potential effect of operant shaping of the responses was a particularly important issue to consider.

While several other investigators have looked at eye movements made to remembered or fictive targets (Becker & Fuchs, 1969; Skavenski & Steinman, 1970; Hikosaka & Wurtz, 1983; White & Sparks, 1986), little analysis as been done concerning the nature of the spatial distortions inherent in these movements. Furthermore, use of the remembered eye movement task has found utility as an experimental tool for neurophysiological studies as a means of temporally separating visual and motor behavior and for studying memory related events (e.g. Mays & Sparks, 1980; Gnadt & Andersen, 1988; Funahashi, Bruce & Goldman-Rakic, 1989). Despite this, there has been little published quantitative analysis of these eye movements. We describe here that there are quantitative differences in the metrics of these movements which may have practical consequences concerning their use as an experimental tool. A preliminary report of these data has appeared previously (Gnadt, Bracewell & Andersen, 1987).

METHODS

Three *Macaca mullata* monkeys and five humans were trained to fixate and look towards small spots of light projected onto a tangent screen. Eye movements were monitored by the scleral search coil technique (Robinson, 1983). In the monkeys the search coils were surgically implanted onto one eye (Judge, Richmond & Chu, 1980). For humans, a coil embedded in an annulus contact lens was used (Collewijn & Van der Mark, 1975).

The monkeys were trained and utilized for data collection for 5–10 months. Two of the monkeys were used for additional neurophysiological experiments, one of which was analyzed retrospectively from previously collected data (Andersen, Essick & Siegel, 1987). Animals were maintained on standard laboratory chow *ad libitum* and received their daily fluids as rewards during training and experiments. Aseptic surgical procedures were used to mount a painless head restraining device and a scleral eye coil on each monkey.

The human subjects were graduate and professional students (age 18–30) recruited for their tolerance to the contact lens. There were four males and one female. Once the subjects had received instructions about the task, the contact lens was inserted and the subjects were given 5 min of practice and acclimation to the apparatus. Data was collected for about 30 min and the contact lens was removed. Two of the subjects participated in multiple recording sessions. The subjects' heads were fixed by means of a bite bar.

Electrophysiological methods

Visual stimuli were presented by a system of three projectors which focused light spots of various sizes onto a rear projection screen located 57 cm in front of the subjects. Mirror galvanometers under the control of a PDP-11 lab computer positioned the images on the screen. Shutters controlled the appearance and disappearance of the targets. During experiments, the spots were 0.4 deg in diameter adjusted to 15 cd/m^2 using neutral density filters. All experiments were performed in a completely dark room except for the control experiments, described below, which investigated the effect of additional visual cues in the environment.

The eye monitoring system was accurate to values of less than 0.25 deg with a range greater than ±40 deg from straight ahead. Eye positions associated with rotations of the eye far from parallel to the magnetic fields were corrected off-line using appropriate sine and cosine correction factors. Eye positions were sampled at 500 Hz, except for the retrospective data from the one monkey (M02) which was sampled at 100 Hz. Eye velocities were calculated off-line from the eye position signal using a second order differentiating/filtering algorithm (Usui & Amidror, 1982). Eye velocity criteria were utilized in monkey M02 to define the start and end points of the saccades (see below). However, due to the filtering characteristics of this low sample rate, peak eye velocities for this monkey were not compared quantitatively with the other subjects.

Behavioral training

The appropriate oculomotor behaviors were trained and maintained in the monkeys by rewarding the animals with fruit juice for successfully completing the appropriate eye movements. Stringently confined fixations at various positions on the screen were used to calibrate the eye monitoring system at the beginning of each session and following any adjustments during sessions. Calibration data were retained for verification and calibration of off-line analyses.

Once the monkeys were reliably trained to make visually guided saccades, they were trained to make quick eye movements to remembered visual targets, as first described by Hikosaka and Wurtz (1983). In the remembered target task, one spot appeared (the fixation spot) and the monkey acquired and maintained fixation of that target for as long as it remained on. Then a second spot appeared at some eccentric position for 300 msec but the trial was aborted and no reward delivered if the monkey failed to maintain fixation of the first spot. Finally, 400 msec or more later, the fixation spot was extinguished and the monkey was rewarded for looking toward the former location of the second target within a specified accuracy and for maintaining fixation in the dark for an additional 500 msec. We will refer here to the two tasks as the visual target task and the remembered target task.

Early in the training, the window of allowable targeting accuracy was large (approx. 30 deg) and the remembered target task was interleaved with the visually guided task. Within 1–2 weeks this window was reduced in size and the interleaving was no longer required. For one monkey (M13) the final size of this window was ±10 deg. Several attempts were made to decrease the size of this window further. However, due to persistent targeting errors, described in the results below, it was not possible to reduce this window further. For monkey M88, the window was maintained at ±22 deg in the vertical and ±18 deg in the horizontal over the period of post-training data collection.

Monkey M02 had been trained to make eye movements using an entirely different training procedure and task. This was an important control to investigate the generalizability of the results to other behavioral strategies and other requirements of oculomotor control. It also represents an extreme opposite situation to the highly permissive training in terms of feedback of performance which was used for M88. This monkey was trained to pull a lever upon detection of the fixation spot projected on the screen. A second target spot appeared, similar to the task described above, while the monkey was required to maintain fixation of the first spot. Following the saccade to the remembered target location, the target light would come back on and the monkey released the lever in response to a slight dimming near the threshold for detection. Invariably, the monkey would correct any errors when the target reappeared by looking to it. Thus, this monkey received visual feedback of targeting accuracy at the end of every trial.

For the human subjects, careful instructions of the desired tasks were substituted for the extended training necessary for the monkeys. For the remembered target task, subjects were told to continue looking at the initial fixation spot until it was extinguished. During the period of fixation a second "target" spot would be presented, but they should not look towards it until the first spot was turned off. At that time they should look to the former location of the target spot as accurately as possible. For the visually guided task, subjects were instructed to look accurately at the spot and to quickly re-acquire the target if it moved. Verbal feedback that the subjects were performing the appropriate behaviors was provided during the initial 5 min of practice. After that, no further feedback of performance was provided.

Data analyses

Representative data were selected from the various sessions for quantitative analysis. For each task type, two blocks of trials collected on separate days were selected and combined for analysis. One of the two blocks was selected blindly from a list of days in the early months of data collection after training was complete and the other from the later months of experiments. This ensured that results peculiar to a particular day did not confound the experimental manipulations. Generally, each block consisted of 70–140 trials with approx. 6–15 trials for each level of the variables tested. The sequence of presentation among variables was varied pseudo-randomly. Except where noted, statistical comparisons were performed between appropriate tasks collected on the same pair of days. The analysis of variance (ANOVA) was used to test differences between multilevel variables. Comparisons between group means (including *post hoc* analyses from the ANOVA) were performed using the t-test, adjusting the degrees of freedom for unequal variances where necessary (Welch's correction). To avoid type II statistical errors (false positives), results of the *post hoc* analyses were considered significant only if they exceeded a level of $P < 0.01$. Differences between group variances were analyzed using the F-test. Analysis of coefficients of linear correlation were calculated for a few *post hoc* comparisons. Due to unknown factors, small magnitude (less that 0.5 deg) differences occasionally were present for equivalent tasks on different days. For this reason and because the size of the stimulus spots were 0.4 deg, statistically significant differences having an absolute magnitude of effect less than 0.5 deg could not be attributed to the experimental manipulations.

Data were analyzed by searching the trials for the saccades based on eye speed criteria. Eye speed was calculated as the instantaneous rate of change in eye position in the direction of movement (tangential eye velocity). The beginning of the saccade was defined as the point at which the eye speed exceeded 35 deg/sec. The end of the movement was determined as the point at which the eye speed dropped below a sustained 50 deg/sec for the monkeys and 35 deg/sec for the humans. This second eye speed cutoff was determined empirically as the optimal value to differentiate saccades (which often decelerated slowly during remembered saccades) and the post-saccadic drift which sometimes followed the remembered saccades (see Fig. 2). The end position of the saccade was defined as the average eye position for the 50 msec following the return to the low eye speed cutoff. Thus, certain types of systematic post-saccadic drift during this 50 msec could influence the end position value. These events were relatively rare and occurred only up to a maximum magnitude of about 1 deg when they did occur. Random post-saccadic drift and corrective saccades did not influence the determination of the end position of the movement. In order to measure oculomotor performance unique to the remembered target task, targeting error was determined as the difference in vertical and horizontal component of the end position of the remembered saccade relative to the end position of the saccades to visual targets during the same recording session.

A series of experiments were performed to address the following questions: (1) what are the quantitative differences in targeting accuracy for saccades to remembered targets versus those to visual targets? A statistically reliable difference would indicate that the spatial sensorimotor transformation is not the same between the two tasks; (2) are there effects of initial eye position on the spatial transformation? Finding eye position effects would indicate that some aspect of the sensorimotor transformation which involves orbital position factors is different between the two tasks; (3) do head position factors effect the metrics of the eye movements? Finding effects of head position would suggest that either somatic or otolith factors can influence this visual sensorimotor transformation; (4) do nontarget visual cues influence the metrics of the movements? It is of interest whether targeting accuracy in this task is influenced by nontarget visual cues since most models of visual sensorimotor transformation do not include visual factors other than those specific to the target; (5) what is the time course of the accumulation of spatial distortions inherent in the remembered saccades? These data provide some insight into the time course of the differences in the sensorimotor processing between the two tasks, thus providing constraints for future neurophysiological investigation and for computational models.

Experimental procedures

The two types of movements were compared for eccentricities of 10, 15, 20 and 30 deg with the movements originating from a position straight ahead. In most cases, within a block of trials the target eccentricity was fixed and the direction varied pseudo-randomly to one of eight possible directions. The eight directions included the horizontal and vertical meridians and the four directions along the 45 deg diagonals. Not all directions or eccentricities were tested in each subject. For some cases, for blocks of trials having targets at 15 deg eccentricity along the meridians, targets with 21 deg eccentricity (15 deg vertical and 15 deg horizontal displacement) were interleaved for the diagonal directions.

For tests of the effects of initial eye position, remembered targets of 15 deg eccentricity were performed for different initial eye positions. For tests of the effects of head position, targets of 15 deg eccentricity were performed with the head rotated relative to the shoulders. These trials were performed only on monkey M88 and were not tested on the humans. The head was rotated manually by the investigator and fixed in positions 15 deg along the meridians. To ensure that virtually all of the manipulation was restricted to rotation of the head at the neck, quantitative analyses were performed only for vertical rotations of the head. To avoid the target position distortions due to the differences in target depth of the flat tangent screen, it was necessary to choose appropriate quantitative comparisons. Statistical comparisons were made only between trials grouped such that tangent errors were symmetrical. For example, we made comparisons of horizontal movements for orbital starting positions of straight up and down by 15 deg, or comparisons of vertical movements at symmetrically equal starting positions along the horizontal meridian. For tests of head position effects we compared the different conditions only for movements to the targets directly right and left of fixation.

For tests of the effects of nontarget visual information, one monkey and one human were tested for saccades to remembered targets of 15 deg eccentricity originating from straight ahead with various levels of additional visual information. Eye movements were tested in a dimly lit room where peripheral visual contours in the surrounding environment were available (6.5×10^{-3} cd/m^2 average room luminance). In other trials, additional visual information was added by superimposing on the tangent screen a random dot pattern having 0.5 cm black dots of 1.2 spots/cm^2 density on a white background (average screen luminance $= 8.2 \times 10^{-2}$ cd/m^2). Each condition of visual information was compared to its corresponding visual target control trials.

For investigation of the temporal accumulation of spatial distortions, one monkey and two humans were tested by comparing the spatial errors for the different directions of movement at two different periods of memory-linked delay: 400 msec (plus saccadic latency) vs 1500 msec (plus saccadic latency). In monkey M88, this issue was investigated in more detail by varying the delay more continuously over a wider range of values. The timing of the offset of the target light was shortened relative to the offset of the fixation spot so that the latency from the beginning of the saccade to the offset of the target varied from -2 to 2300 msec. Within a block of these trials, timing varied pseudo-randomly for one direction of movement while this direction of movement was interleaved with occasional trials in another direction. Quantitative analysis was performed on data from targets positioned 15 deg to the right collected on 9 days over a period of 10 weeks.

RESULTS

In Fig. 1 representative eye movements to remembered targets are compared to those in visual targets for one monkey and one human. Note that the movements to the remembered targets often were exceptionally curved in trajectory. These movements also were slower than those to visual targets (see Fig. 8). Additionally, note the gross spatial distortions, which appeared as errors in the mean end positions of the movements relative to the target positions. For the monkeys, there was a generalized upward component added to all the saccades in the remembered target condition. Similar, though less dramatic, systematic distortions were often seen in the humans (see Fig. 4). Finally, there also was considerably more inter-trial variability of saccade end position in the remembered target task. This increased variability was statistically significant for all monkey and human

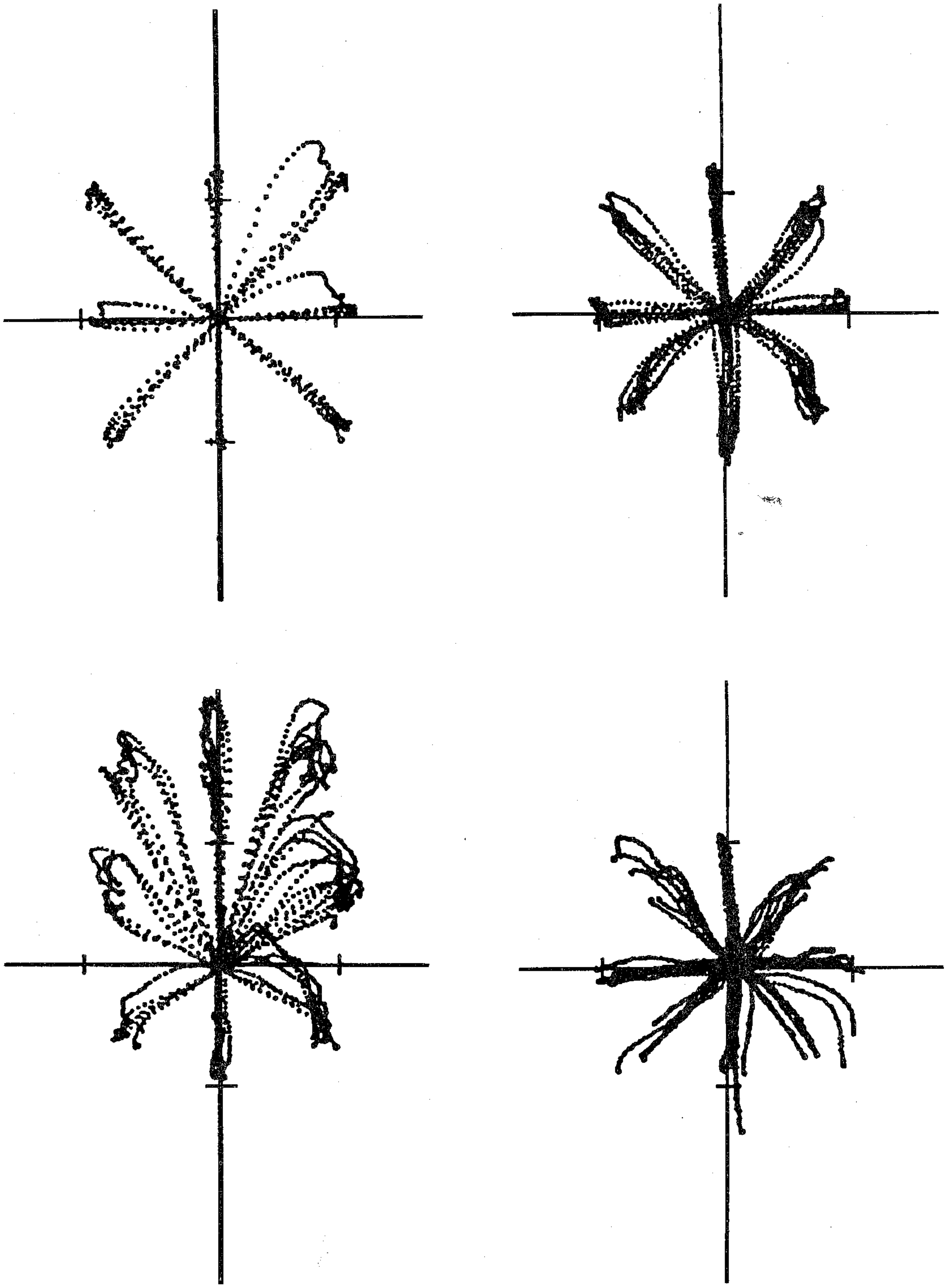

Fig. 1. Comparison of eye movements made to visual targets (top) and those to remembered targets (bottom) for monkey M13 (left) and human H53 (right). Target positions are the same for the two conditions. Each dot represents eye position sampled every 2 msec for 6–10 trials for each target. Scale marks = 15 deg.

subjects (individual F-tests, $P < 0.01$). Figure 2 shows the movements to remembered targets for 32 target positions at the various eccentricities for monkey M88. This monkey had a peculiar post-saccadic drift for movements down and to the right. For all subjects, both monkey and human, there were consistent spatial errors in looking toward the remembered targets. These errors provided an indication of the spatial distortion which accumulated during the

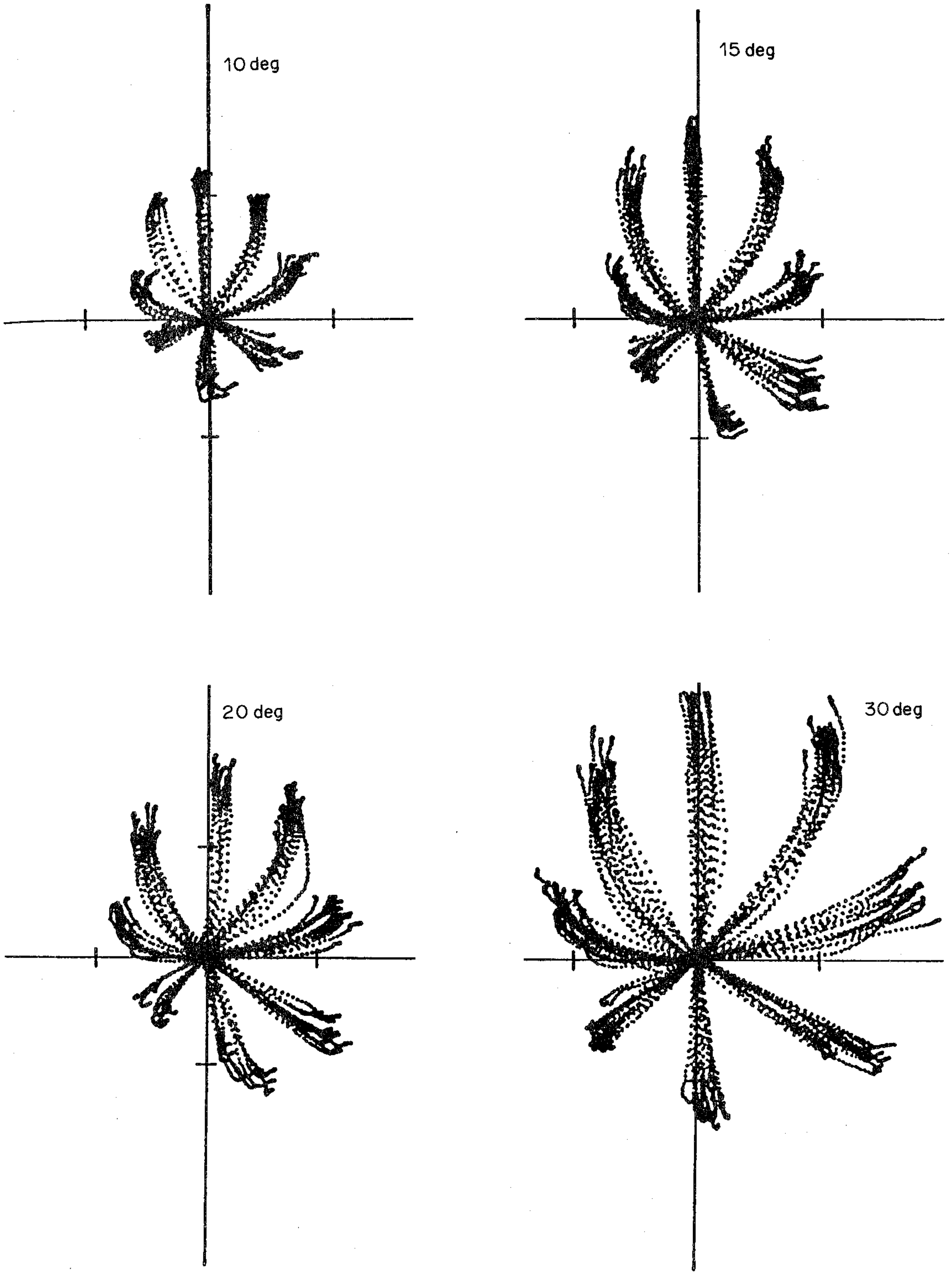

Fig. 2. Comparison of eye movements to remembered targets for the various eccentricities for monkey M88. Targets were arranged symmetrically in the various directions at the eccentricities indicated. Scale marks = 15 deg.

memory-linked delay. A summary diagram of the spatial distortions for each monkey is shown in Fig. 3. Similar, though smaller, distortions were present in the humans and are shown in Fig. 4. The mean errors are illustrated in these figures as the length and direction of the error lines associated with each target position.

As shown in Table 1, there were significant errors in either the horizontal or vertical position component for each subject, except one

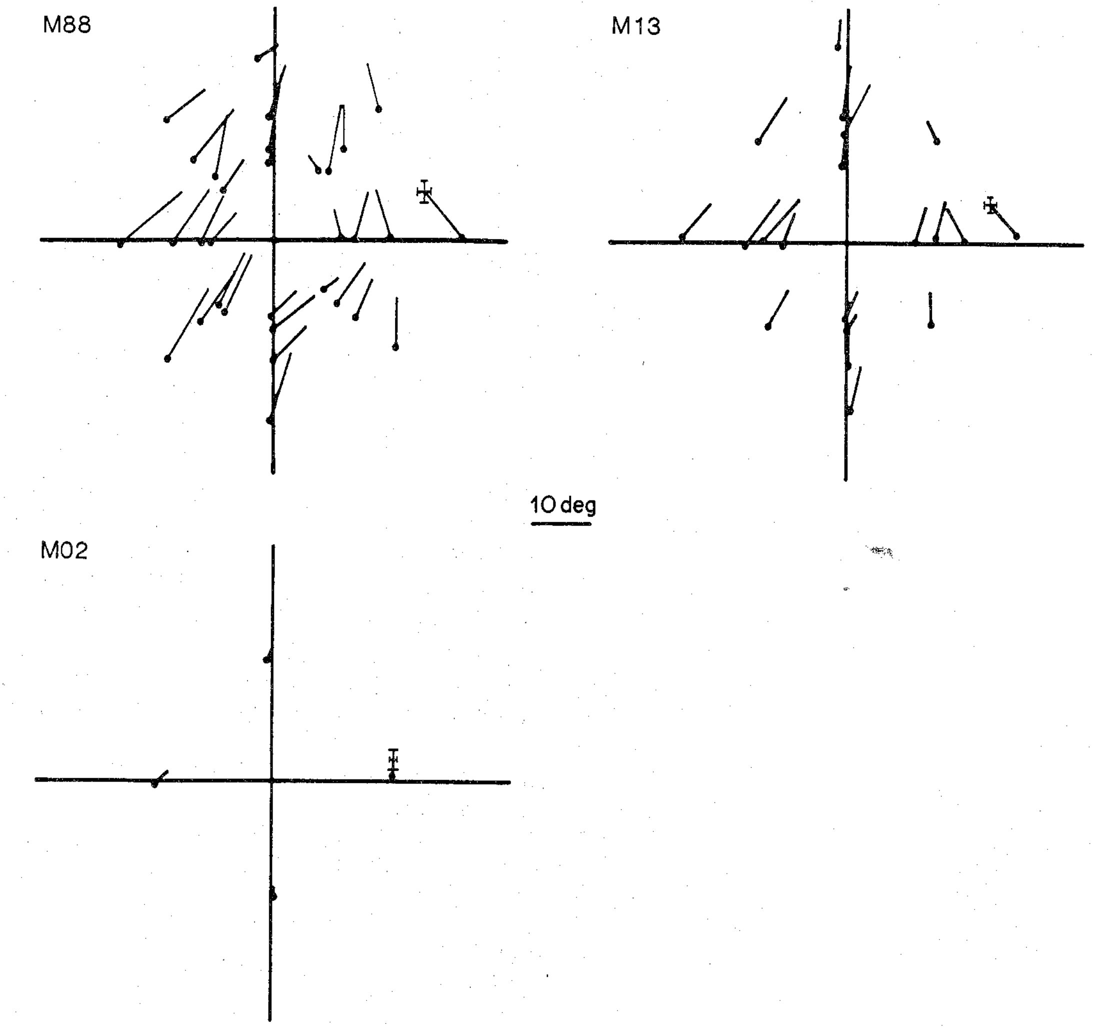

Fig. 3. Summary diagram of the spatial distortions for each monkey. The solid circles represent the various target locations. The associated lines indicate the direction and magnitude of targeting error for that remembered target location. The uncircled end of the line is placed at the mean end position of the remembered saccades to that target. The weighted average standard deviation for all of the targets has been indicated as error bars on one of the targets for each monkey.

human. This distortion was not a uniform shift in end position of the movements. There was a significant interaction of the effects of the direction and target eccentricity on the error in both vertical and horizontal components (Table 1). Furthermore, the length of movement error was not a constant fraction of the target eccentricity ("Length/Eccentricity", Table 1), but was highly correlated to the length of the movement (M88, $r = 0.99$; M13, $r = 0.75$; H52, $r = 0.65$; H53, $r = 0.55$). These relationships can be seen graphically in Figs 3 and 4 by noting that the error lines are not parallel or of equal length.

Eye position effects

Monkey M13 was tested using the same directions of movement from nine different positions within the orbits (straight ahead, up and left 15 deg, up 15 deg, left 15 deg, etc.), while monkey M88 was tested for the eight directions of movements at five orbital positions (straight ahead, 15 deg up, down, right and left). One of the human subjects (H54) was tested for orbital position effects in the same fashion as monkey M88.

Representative movements to remembered targets from different orbital positions are shown in Fig. 5. Note the similarities in the movements from the different starting positions. This indicated that the spatial distortions were not due to the subjects looking toward a particular orbital position or a particular position on the screen. Despite these similarities, there were statistical differences in the end position

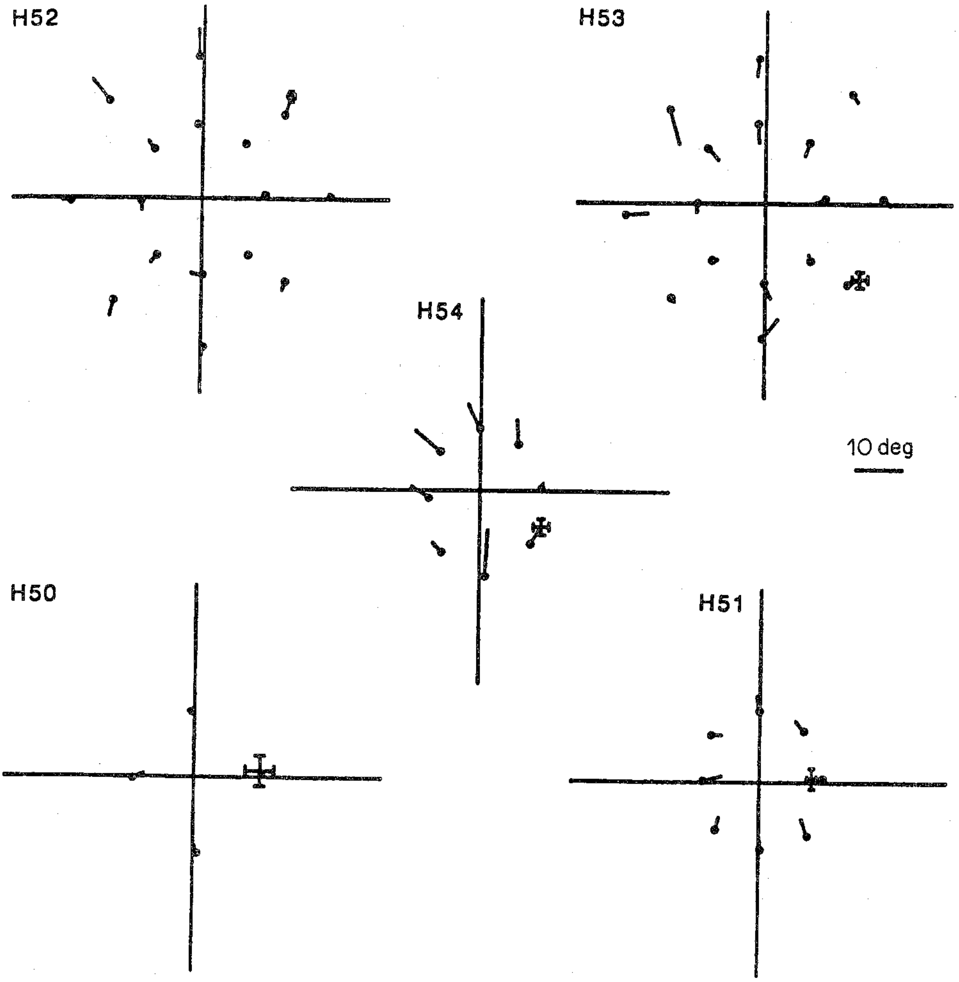

Fig. 4. Summary diagram of the spatial distortions for each human. See Fig. 3 for explanation of symbols.

errors for some of the various starting positions, even when the comparisons were restricted to symmetrically placed movements on the tangent screen. The mean errors and their standard deviations are shown in Table 2. This indicated that even though the spatial distortions were not due to some goal directed phenomenon, the trajectories of movements were affected by eye position. Additionally, careful inspection revealed subtle differences in the dynamic trajectories of certain directions of movement from the different initial positions (see Fig. 5). These differences were not apparent in the saccades to visual targets.

Head position effects

To determine the nature of the effects of head position and its interaction with eye position, the following manipulations were made. Note that only those movements which had appropriately symmetrical changes in depth on the tangent screen were compared statistically (see Methods). The mean end position errors for the various eye/head conditions are shown in Table 3.

(a) "Primary" orbital and head positions. Remembered targets of 15 deg eccentricity at each at the eight directions were tested (along with the control saccades to visual targets) with the eyes and head both in their respective "primary" positions. We use the term primary positions here not in the rigorous sense, but only to indicate that the eyes were directed straight ahead, the head straight on the shoulders with the body erect and body directed straight towards the tangent screen.

(b) Orbital rotation up, "primary" head position. Next, the same movements were tested from a fixation position 15 up on the screen with the head still in its primary position. By rotating the eyes up, the orbital condition had been changed while the head position remained unchanged.

Table 1. ANOVA[a] for target direction and target eccentricity

Subject	Direction of error	Factor	F (degrees of freedom)	Significance level
		Monkeys		
M88[b]	Vertical	DIR*ECCEN	$F(21,1320) = 26.10$	$P < 0.001$
	Horizontal	DIR*ECCEN	$F(21,1320) = 57.92$	$P < 0.001$
	Length/Eccentricity	DIR*ECCEN	$F(21,1320) = 24.58$	$P < 0.001$
M13[b,c]	Vertical	DIR*ECCEN	$F(9,298) = 39.81$	$P < 0.001$
	Horizontal	DIR*ECCEN	$F(9,298) = 87.21$	$P < 0.001$
	Length/Eccentricity	DIR*ECCEN	$F(9,298) = 135.89$	$P < 0.001$
M02[c,d]	Vertical	DIR	$F(3,53) = 0.81$	NS
	Horizontal	DIR	$F(3,53) = 6.15$	$P < 0.01$
		Humans		
H52	Vertical	DIR*ECCEN	$F(7,137) = 33.75$	$P < 0.001$
	Horizontal	DIR*ECCEN	$F(7,137) = 6.51$	$P < 0.001$
	Length/Eccentricity	DIR*ECCEN	$F(7,137) = 11.34$	$P < 0.001$
H53	Vertical	DIR*ECCEN	$F(7,63) = 4.52$	$P < 0.001$
	Horizontal	DIR*ECCEN	$F(7,63) = 1.82$	NS
	Horizontal	DIR	$F(7,63) = 2.27$	$P < 0.05$
	Horizontal	ECCEN	$F(7,63) = 9.29$	$P < 0.001$
	Length/Eccentricity	DIR*ECCEN	$F(7,63) = 4.66$	$P < 0.001$
H54[d]	Vertical	DIR	$F(7,43) = 12.99$	$P < 0.001$
	Horizontal	DIR	$F(7,43) = 10.63$	$P < 0.001$
H51[d]	Vertical	DIR	$F(7,135) = 1.30$	NS
	Horizontal	DIR	$F(7,135) = 14.15$	$P < 0.001$
H50[c,d]	Vertical	DIR	$F(3,47) = 0.86$	NS
	Horizontal	DIR	$F(3,47) = 0.19$	NS

[a] Null hypothesis (H_0): error is uniform (constant) for each target position. Significant effects indicate that the spatial error is nonuniform. [b] Data was pooled from several different days of recording. [c] Data was available only along the four meridian directions. [d] Only one target eccentricity was tested.

(c) "Primary" orbital position, head rotation up. Then, the head was rotated and fixed 15 deg up with the targets still originating from a position 15 deg up on the screen. Eye movements were now tested starting from the primary orbital position, which due to the rotation of the head was 15 deg up on the screen. In this case, the orbital condition corresponded to the first straight ahead trials, but with the head rotated up.

(d) Orbital rotation down, head rotation up. Finally, with the head rotated up 15 deg, the same movements were tested again, but now originating from the center of the tangent screen. Necessarily, this represented an orbital position 15 deg down with the targets at the center of the screen in the same position with respect to the body as the original straight ahead trials.

The results of the mean targeting errors for these four conditions are given in Table 3. The following three hypotheses were tested concerning the nature of the effects of head position on the spatial distortions during these tasks. These experiments investigate the spatial distortions which were unique to the memory-linked task relative to the visually guided task. The purpose was to use these differences to investigate whether the sensorimotor transformation process includes factors related to head position. Note that it is not necessary for head related factors to effect this visual-to-oculomotor spatial transformation. Head related factors would effect these distortions only if the brain involves somatic or otolith information in the transformation process as part of some higher order spatial frame of reference.

I. Were the differences between saccades to remembered targets and to visual targets independent of eye and head position? If this were true, there would be no differences between the spatial distortions for any combination of different head and eye conditions, which would suggest an oculocentric organization to the spatial distortions. Note in Table 4 that the spatial distortions were affected by an interaction between the eye–head term and the direction of movement. The statistical interaction between target direction and eye–head condition indicated that the distortion was not uniform between the two directions tested. This finding is consistent with the result given above

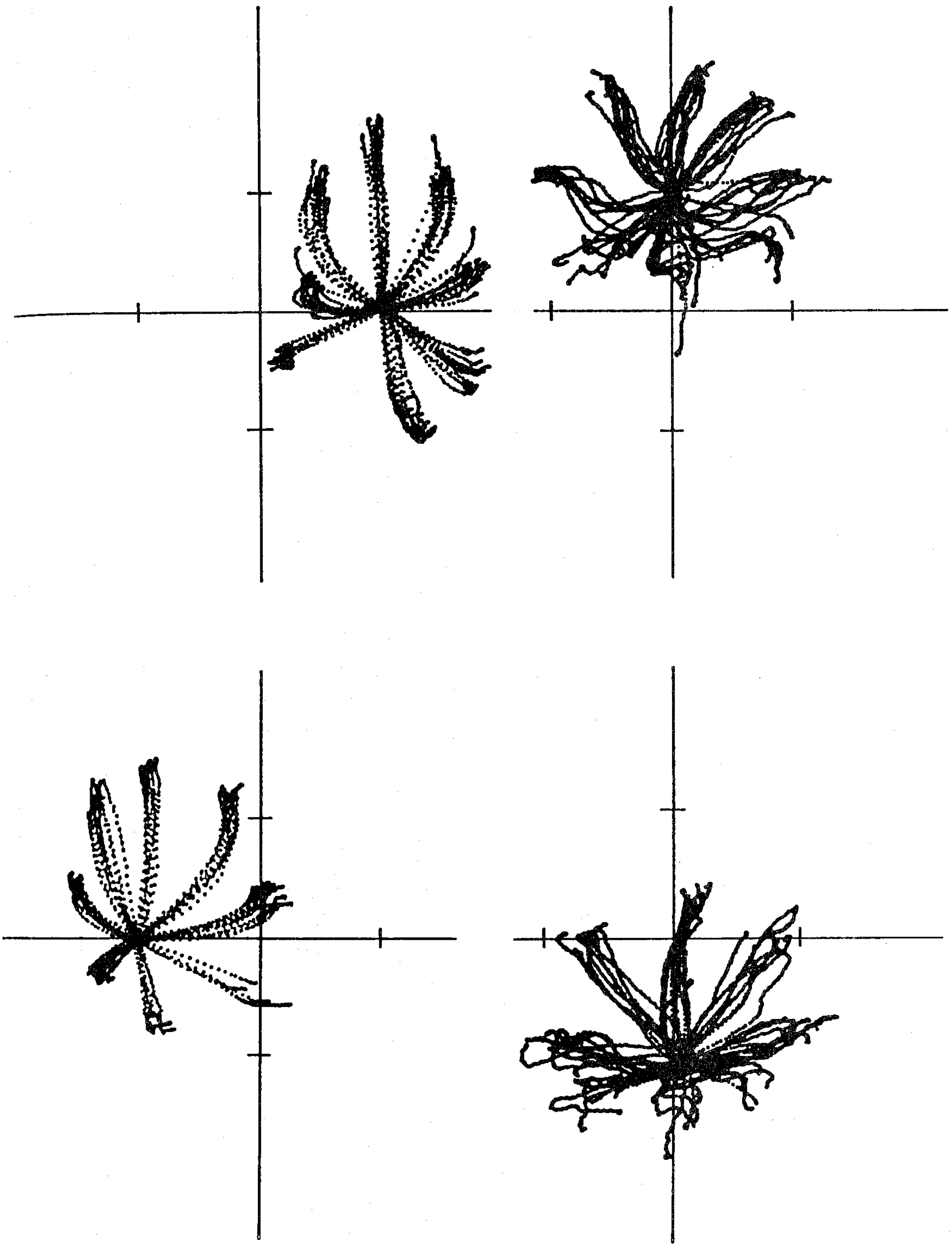

Fig. 5. Comparison of eye movements made to remembered targets for different orbital positions for monkey M88 (left) and human H54 (right). The center of the axes indicates straight ahead. Target eccentricities were 15 deg about the eight symmetrically arranged directions from each initial position. Scale marks = 15 deg.

that there is a significant effect of initial eye position; a result which suggests that the sensorimotor transformation is not oculocentric.

II. Were the distortions the same when the orbital condition was held constant while the head was rotated? A lack of differences would suggest a craniocentric nature to the distortion.

Table 2. t-Tests, effect of eye position[a]

Target position	Direction of error	Mean error (standard deviation) Orbital position		Significance level
		M88		
		Right 15 deg	Left 15 deg	
15 deg up	Horizontal[b]	1.30 (0.89)	−7.63 (7.16)	0.001
	Vertical[c]	7.73 (1.88)	12.16 (4.44)	0.001
15 deg down	Horizontal[b]	4.97 (1.78)	−7.73 (5.17)	0.001
	Vertical[c]	2.57 (2.05)	−16.51 (9.46)	0.001
		Up 15°	Down 15°	
15 deg left	Horizontal[b]	4.64 (1.04)	4.38 (1.49)	NS
	Vertical[c]	5.19 (1.50)	8.87 (1.78)	0.001
15 deg right	Horizontal[b]	0.03 (1.42)	2.42 (2.06)	0.001
	Vertical[c]	4.97 (1.54)	8.96 (1.38)	0.001
		M13		
		Up 15°/Left 15°	Down 15°/Left 15°	
15 deg right	Horizontal[b]	2.44 (1.44)	0.97 (0.86)	0.01
	Vertical[c]	5.22 (1.41)	4.70 (0.67)	NS
		Up 15°	Down 15°	
15 deg right	Horizontal[b]	−1.90 (5.12)	−0.62 (0.89)	NS
	Vertical[c]	5.14 (2.15)	5.10 (1.40)	NS
		Up 15°/Right 15°	Down 15°/Right 15°	
15 deg right	Horizontal[b]	−4.90 (8.49)	−4.05 (0.71)	NS
	Vertical[c]	2.40 (6.55)	7.22 (4.90)	NS
		Up 15°/Left 15°	Up 15°/Right 15°	
15 deg up	Horizontal[b]	2.12 (0.45)	0.35 (0.72)	0.01
	Vertical[c]	10.63 (2.41)	10.12 (1.31)	NS
		Left 15°	Right 15°	
15 deg up	Horizontal[b]	2.42 (0.56)	0.47 (0.88)	0.001
	Vertical[c]	7.12 (2.07)	8.21 (1.78)	NS
		Down 15°/Left 15°	Down 15°/Right 15°	
15 deg up	Horizontal[b]	1.62 (0.60)	1.50 (0.46)	NS
	Vertical[c]	8.69 (1.98)	7.86 (2.63)	NS
		H54		
		Up 15°	Down 15°	
15 deg left	Horizontal[b]	−2.18 (3.94)	−3.90 (2.79)	NS
	Vertical[c]	0.81 (3.51)	2.87 (1.09)	NS
15 deg right	Horizontal[b]	2.52 (2.06)	2.65 (1.84)	NS
	Vertical[c]	0.43 (1.06)	2.09 (1.28)	0.01

[a] Comparison of mean errors for different orbital positions at target positions where tangent screen effects were symetrical. [b] Horizontal error: + ⇒right; − ⇒left. Note that for rightward movements: + ⇒hypermetria; − ⇒hypometria, while the opposite is true for leftward movements. [c] Vertical error: + ⇒up; − ⇒down. Note that for upward movements: + ⇒hypermetria; − ⇒hypometria, while the opposite is true for downward movements.

A significant difference, however, would indicate an effect of head position, thus suggesting a somatotopic organization. This was tested by comparing the spatial distortions between the first straight ahead condition and the condition where the targets were 15 deg up on the screen with the head rotated 15 deg up. This test revealed a significant interaction of target direction and head position, but only for the vertical component of the movements (Table 4).

III. Would eye and head position factors add linearly to provide an invariant somatocentric frame of reference? This was tested by comparing the end position errors for targets which appeared in the same position on the screen, regardless of the various combinations of eye and head position. This comparison was made

Table 3. Mean error, target direction and eye–head condition

Target direction	Direction of error	Mean	Standard deviation
"Primary" orbital and head position			
15 deg left	Horizontal[a]	3.90	1.10
	Vertical[b]	10.49	1.28
15 deg right	Horizontal[a]	5.02	1.97
	Vertical[b]	7.69	1.47
Orbital position up and "primary" head position			
15 deg left	Horizontal[a]	4.81	0.67
	Vertical[b]	10.15	1.79
15 deg right	Horizontal[a]	1.35	2.08
	Vertical[b]	9.44	3.89
"Primary" orbital position and head position up			
15 deg left	Horizontal[a]	4.42	1.24
	Vertical[b]	9.41	1.70
15 deg right	Horizontal[a]	4.71	1.60
	Vertical[b]	4.54	2.25
Orbital position up and head position down			
15 deg left	Horizontal[a]	3.21	0.94
	Vertical[b]	10.19	0.95
15 deg right	Horizontal[a]	5.01	1.85
	Vertical[b]	6.76	2.09

[a] Horizontal error: + ⇒right; − ⇒left. Note that for rightward movements: + ⇒hypermetria; − ⇒hypometria, while the opposite is true for leftward movements.
[b] Vertical error: + ⇒up; − ⇒down.

first by testing the distortion in the orbital rotation up vs head rotation up conditions. Then, this comparison could be tested again using the first condition having both eyes and head in their primary positions vs having the head position up and orbital position down by opposite and equal amounts. These two tests revealed different results. There was significant interaction of target direction and eye–head condition when the effects of equal upward rotation of eye vs head rotation was tested (Table 4). However, when the same hypothesis was tested using equal but opposite rotations of eyes and head, there was no signficant interaction or main effect of the eye–head condition. These seemingly contradictory findings indicate either that the condition of opposite and equal rotation failed to reach levels of statistical significance (a "false negative" statistical error) or that the interaction between the ocular and head rotation is nonlinear.

Movement dynamics

Qualitatively, it was noted that there was a great variability of the eye velocity profiles for the remembered targets. Particularly, the variability of the timing of the velocity profiles of the horizontal and vertical components was a hallmark of the movements to remembered targets. It is this variability between the horizontal and vertical velocity components which accounts for the frequently curved trajectories of the movements.

For any length of movement the saccades to remembered targets generally were slower than

Table 4. ANOVA[a] for target direction and eye–head factors

Direction of error	Factor	*F* (degrees of freedom)	Significance level
Three null hypotheses (H_0) were tested:			
H_0: no effect of eye or head position—oculocentric organization (orbital and head positions at "primary" positions, orbital position up, head position up, orbital position down, with head position up):			
Horizontal	DIR*EYE–HEAD	$F(3,155) = 30.42$	$P < 0.001$
Vertical	DIR*EYE–HEAD	$F(3,155) = 8.69$	$P < 0.001$
H_0: no effect of head position—craniocentric organization ("primary" head position, head position up):			
Horizontal	DIR*HEAD	$F(1,80) = 2.00$	NS
Vertical	DIR*HEAD	$F(1,80) = 9.71$	$P < 0.01$
Horizontal	HEAD	$F(1,80) = 0.71$	NS
H_0: linear addition of eye and head effects—somatocentric organization:			
(1) eye and head position manipulated equally (up 15 deg):			
Horizontal	DIR*EYE–HEAD	$F(1,79) = 40.58$	$P < 0.001$
Vertical	DIR*EYE–HEAD	$F(1,79) = 17.29$	$P < 0.001$
(2) eye and head position manipulated opposite and equal (eye down 15 deg–head up 15 deg):			
Horizontal	DIR*EYE–HEAD	$F(1,80) = 1.14$	NS
Vertical	DIR*EYE–HEAD	$F(1,80) = 0.99$	NS
Horizontal	EYE–HEAD	$F(1,80) = 0.27$	NS
Vertical	EYE–HEAD	$F(1,80) = 3.93$	NS

[a] Tests of the effects of eye and head rotations where tangent screen effects were symmetrical.

those to visual targets (see Fig. 8), as has been reported by others (Becker & Fuchs, 1969; White & Sparks, 1986; Rohrer, White & Sparks, 1987). Nonetheless, the velocities of the movements were above those for other types of movement (vergence, pursuit, etc.) and appeared saccade-like in most respects. Additionally, neurophysiological studies using these movements have shown that the same neurons active for "normal" saccades are active during these movements as well (Mays & Sparks, 1980a,b; Hikosaka & Wurtz, 1983; White & Sparks, 1986; Rohrer et al., 1987; Gnadt & Andersen, 1988; Funahashi et al., 1989). It seems quite justifiable to consider these movements as saccades, an assumption that has been made by others as well.

The accumulation of the targeting error as a function of memory-linked delay is shown in Fig. 6. These data were for movements to a remembered target 15 deg to the right for monkey M88. Since most of the error for this direction of movement was in the vertical direction, the vertical component of targeting error is shown. A similar, though smaller magnitude, horizontal hypometria occurred as well. It can be seen that the error began to accumulate within 100 msec of delay and that 80% of the error accumulated within the first 800 msec. A relatively smaller additional accumulation occurred during the following 2000 msec. The inter-trial variability (variance) also followed a similar time course.

A significant interaction of the length of the memory-linked delay and the different directions of movement, as investigated in M13, indicated that the distortions changed nonuniformly for the different directions over time: horizontal, $F(7,652) = 40.39$, $P < 0.001$; vertical, $F(7,652) = 10.6$, $P < 0.001$. This same analysis in humans revealed similar conclusions: H52, horizontal, $F(7,143) = 75.3$, $P < 0.001$; vertical, $F(7,143) = 83.0$, $P < 0.001$; H53, horizontal, $F(7,66) = 2.1$, NS; vertical, $F(7,66) = 5.4$, $P < 0.001$.

Effect of additional visual cues

The effect of the different visual cue conditions on mean end position errors, the behavioral variability and the curved trajectories can be seen in Fig. 7 for the monkey tested under these conditions. The addition of nontarget visual cues improved performance significantly [$F(14,626) = 9.00$, $P < 0.001$]. This significant interaction with direction indicates that the improvement was nonuniform for the different directions of movement. Note that the spatial distortions were the greatest for the movements performed in complete darkness, as well as having significantly greater behavioral variability [horizontal, $F(207,215) = 9.11$, $P < 0.001$; vertical, $F(207,215) = 4.08$, $P < 0.001$]. Also, the maximum eye speeds were most diminished in this condition (Fig. 8).

The errors and the post-saccadic drift was smaller when the room lights were turned on (Fig. 7); however, errors due to spatial distortion was still present for every target position (multiple t-tests, $P < 0.001$). The inter-trial variance was greater [horizontal, $F(164,193) = 10.84$, $P < 0.001$; vertical, $F(164,193) = 3.59$, $P < 0.001$], and the eye speeds were decreased relative to the corresponding control trials to visual targets (Fig. 8). Furthermore, inspection of the dynamic trajectories of the individual movements revealed improvement over the dark condition, though still having substantial curvedness.

When the random dot texture was superimposed on the screen, the curvedness of the movements appeared to improve to levels near that of movements to visual targets (Fig. 7). Maximum eye speeds also were nearly the same as those to visual targets (Fig. 8). Despite this, a small but significant targeting error persisted for one or the other position component of each target location (multiple t-tests, $P < 0.001$), as well as an increased variability of performance [horizontal, $F(150,276) = 1.89$, $P < 0.001$; vertical, $F(150,276) = 4.93$, $P < 0.001$].

As found for the monkey, there also was a nonuniform improvement in performance with additional cues for the human tested under these conditions. However, this nonuniformity was present only in the vertical domain, $F(14,158) = 8.7$, $P < 0.001$. The improvement in the horizontal domain was significant, but uniform, $F(2,158) = 6.6$, $P < 0.01$.

DISCUSSION

These studies have shown that, compared to eye movements made to continuously visible targets, movements made to remembered targets are grossly spatially distorted, often are markedly curved in trajectory, are more variable, and have reduced velocities. The spatial distortions have both a constant and variable component. The constant component generally consists of an upward shift in the end point of

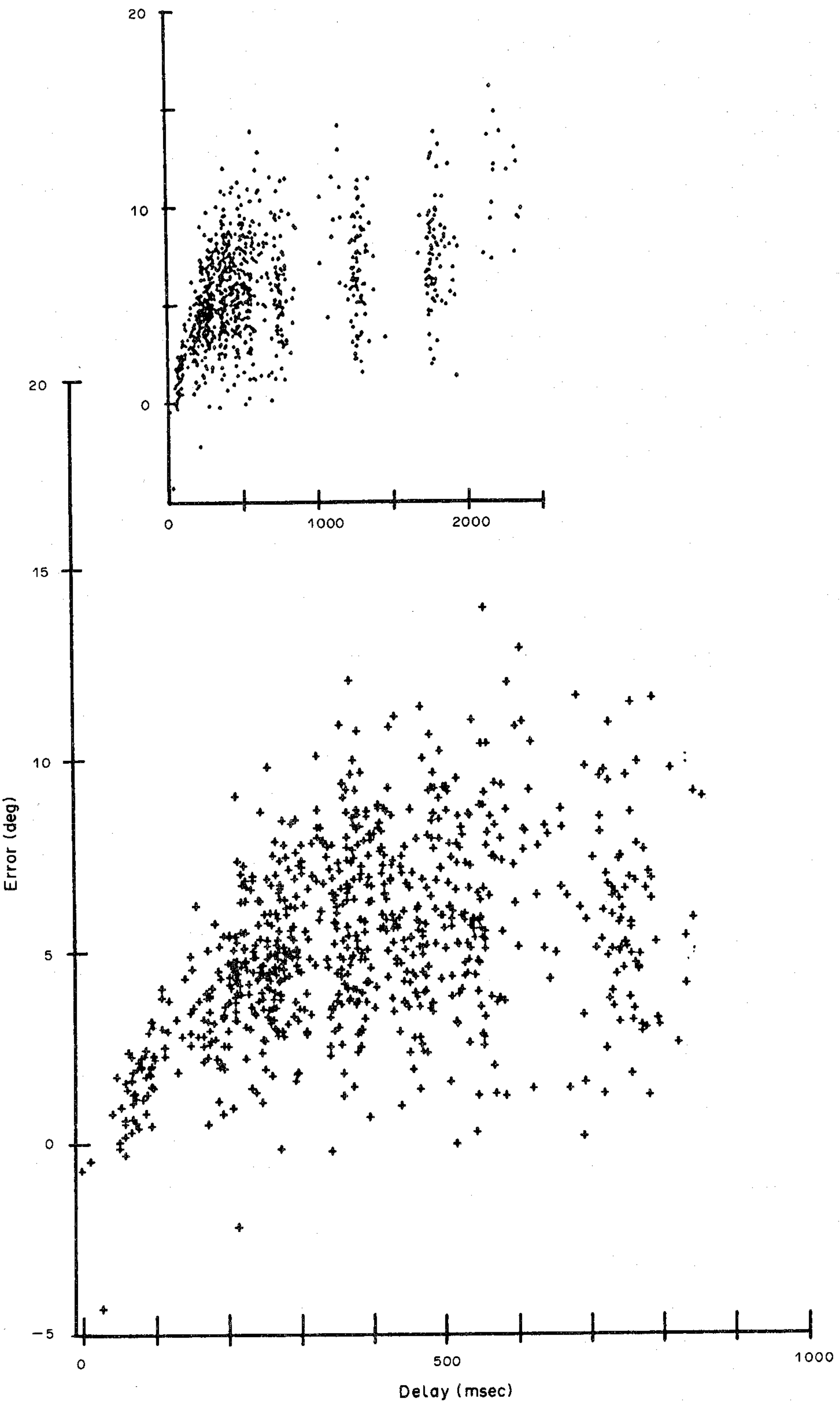

Fig. 6. Accumulation of targeting error as a function of memory-dependent delay (M88). Ordinate = vertical component of targeting error for movements 15 deg to the right. Abscissa = time delay between offset of target and beginning of the saccade. Inset includes the same data on an expanded time scale.

all saccades, resulting in upward saccades being hypermetric and downward movements being hypometric. The spatial distortions and certain dynamic aspects of the movements are effected by eye and head position, and are critically dependent on the presence or absence of the

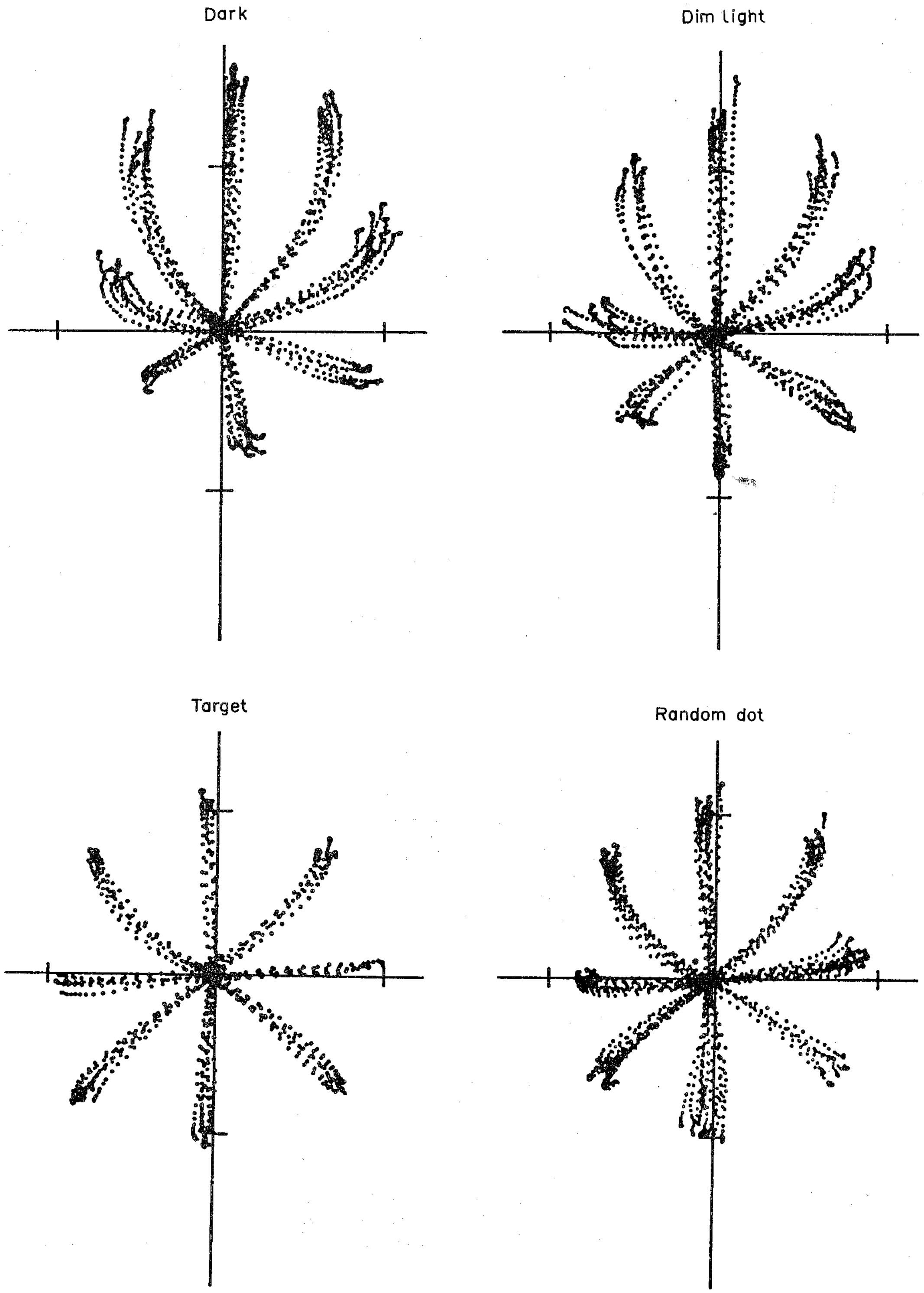

Fig. 7. Comparison of movements to remembered targets under different visual cue conditions (M88). Target locations were the same for all conditions at 15 deg eccentricity. Dark = no ambient light; dim light = dim room illumination; random dot = textured image on screen; target = saccades to visual targets. Scale marks = 15 deg.

target itself. The distortions accumulate relatively rapidly over the first 800 msec of memory-linked delay with a slower increase after that. Furthermore, they are nonuniformly dependent on the direction of movement.

These findings provide us with several insights into the nature of the visual-motor coordinate

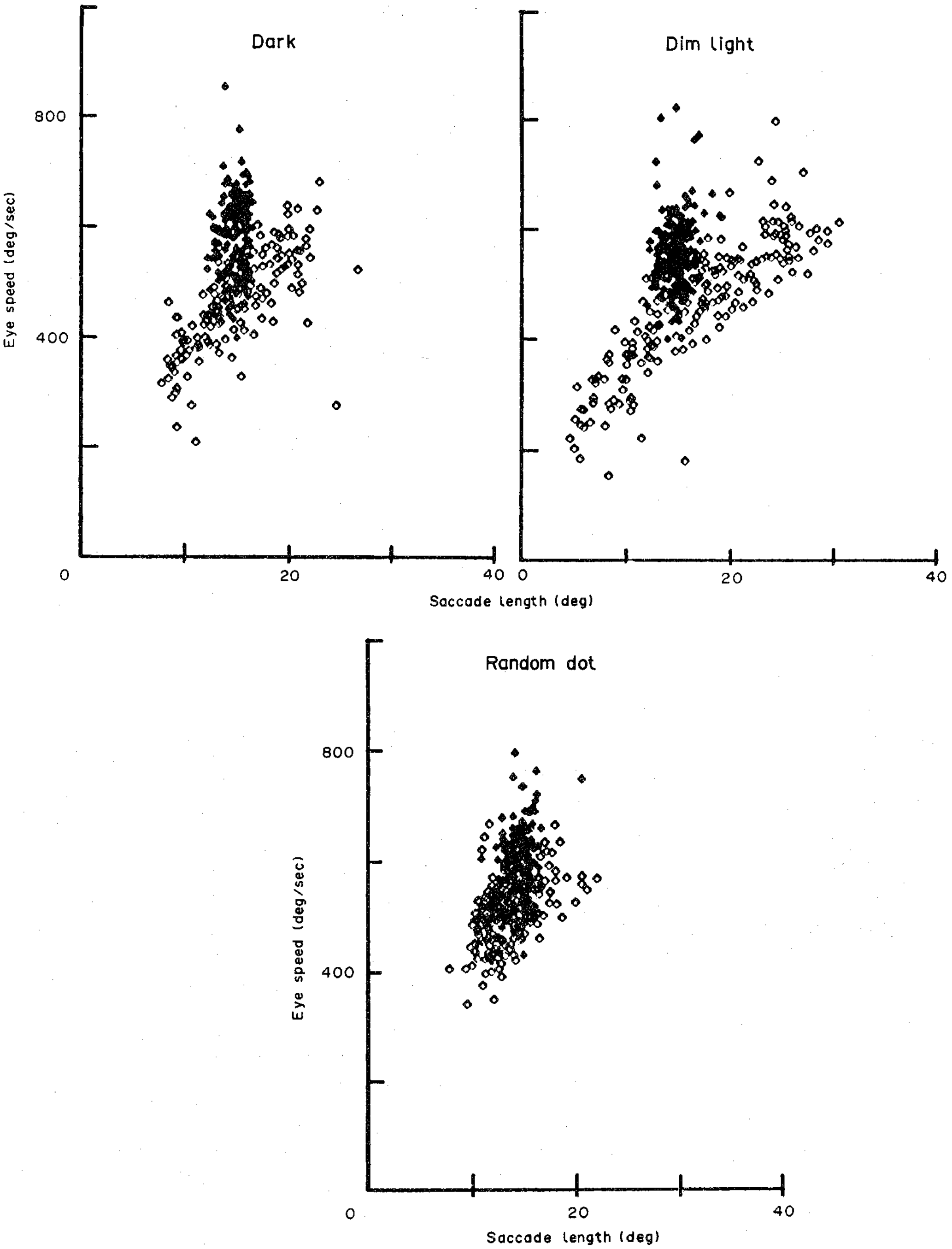

Fig. 8. Comparison of peak eye speeds for saccades to visual and to remembered targets for each visual cue condition in Fig. 6. Solid symbols = saccades to visual targets. Open symbols = saccades to remembered targets. All directions are included. Ordinate = peak eye speed (tangential eye velocity). Abscissa = length of the movement.

transformations which the brain must solve to perform this task. It is important to recall here that error in oculomotor performance represents the error in the sensorimotor transformation in response to identical input demands. There is no obligatory reason that these two processes would have to produce different output. Furthermore, simply adding noise to a linear visual-motor process (perhaps due to some "fuzziness" inherent in memory) would produce only higher variability and not systematic shifts in mean end positions. The peculiar spatial distortion of the end positions suggests that either (1) the "memory" of the retinotopic map of space becomes shifted relative to real gaze direction of the eyes; or (2) that the "memory" of intended eye movement targets does not retain accurate retinotopic registration. Since the spatial distortions were not uniform in the several directions of movements tested, these data support the latter.

The significant effects of initial eye position on the memory-linked spatial distortions indicates that the coordinate frame of reference is not oculocentric. These differences, however, could be due either to *addition* or *omission* of orbital factors. The distortion could be due to expression of eye position factors that normally are balanced out or suppressed. Alternatively, it could be due to omission of eye position factors otherwise present; for example, factors that normally would compensate for nonlinearities of the oculomotor plant. In either case, we know that the distortions are neural in origin, since the spatial input demand and the motor plant have the same physical properties in both tasks.

The experiments with rotation of the head showed that the distortion includes factors related to head position as well. There were differences in end position errors for different positions of the head, even when orbital position was held constant. Apparently this visual to oculomotor spatial transformation has access to information about the orientation of the head; information that would be superfluous purely for orientation of the eyes within the fixed reference of the orbits. It can not be determined here whether these factors might originate from proprioceptive sense, the otolith organs, or even cognitive factors. However, similar effects of body position on attempts of fixation in the dark have been noted by others (Skavenski & Steinman, 1970). Additionally, our data show that, in at least some cases, the eye and head position effects do not add linearly. It currently is not clear what the significance of this latter finding might be, though it suggests the interaction of various frames of reference might be complex.

There was a constant upward bias for the memory-contingent saccades for most saccade directions for all the monkeys and for several of the humans. It is difficult to know the significance of this upward bias. In some cases, where the fixation light was turned off briefly but the monkey was required to maintain fixation at that location, we observed an upward drift in eye position. This drift in the dark often was of similar magnitude and time course as the accumulation in average constant error seen in the memory saccade task. This slow upward drift, often associated with occasional downward quick phases, has been referred to as a "dark nystagmus". One possibility is that the subjects perceived an upward shift of the visual field in the dark which is reflected behaviorally in the upward drift of the eyes. A similar dark drift was reported by Maldonado and Schlag-Rey (1982) for monkeys. They also found, with the head free, that the drift could be expressed as an eye movement, a head movement or both. It would be interesting to test in humans, while fixating in the dark, to determine if the perceived locations of remembered targets drift with time. A positive result would suggest that the upward bias for the constant saccade error we observed is due to a perceived drift in the remembered location of the target.

In considering the experiments which investigated the effect of additional, nontarget visual cues, it is clear that salient visual contours in the environment did not substitute for the visual presence of the target. However, nontarget visual spatial cues did produce some reliable improvement in the distortions, a finding that models of visual-motor transformation ultimately must be able to take into account. By adding an amorphous visual texture to the field on which the movements were made improved performance considerably, though significant error still persisted in the spatial accuracy. It is possible, if not probable, that the subjects may have been substituting a feature on the textured screen as a surrogate target for the movement. This could explain the improvement in dynamic features of the movement, while the persistent spatial errors may have been due to choosing a screen feature which did not exactly correspond to the real target location.

The finding of the smallest mean error in the monkey with the trial-to-trial feedback of performance and the largest in the monkey with the most permissive training suggests that the memory dependent representation is plastic and improves with training. This is supported by data from attempts in humans to fixate remembered targets in the dark where it has been noted that training and experience can improve performance (Hansen & Skavenski, 1985). Skavenski and Steinman (1970) also found that human subjects were unable to eliminate error in fixation in the dark, even when feedback was available at the end of every trial. These data suggest either (1) that additional brain elements which fail to retain spatial accuracy are involved in the memory-linked task, or (2) that critical elements of the process fail to operate accurately in the absence of visual input. In either case the process appears to be plastic and to be modified by training. This can be seen both in the progress of shaping the accuracy of these movements and in the comparison of accuracy for different levels of training demand.

The permissive training procedure employed in monkey M88 was an important control for this study. It not only documents the effect of performance demand on accuracy, but also demonstrates that we seem to be shaping the natural effort of the monkey to perform the task, and not that we have shaped into the monkeys' behavior an aberrant response which we interpret as a spatial distortion. Consider the following scenario: suppose we had begun training with a highly stringent performance demand. The monkey might make its best attempt at the task, but miss the target and fail to receive reward. If the monkey did not become frustrated too quickly, he might come to learn through trial and error that if he looks to a location 10 deg below where he thinks the target was, then he gets rewarded. In fact, it is possible that the reason we were unable to train monkey M13 to better accuracy may have been related to factors of trying to train the animal to look away from an errantly perceived location of the target. Verbal reports from the human subjects following the recording sessions indicated that they had only a vague perception of how accurately they were able to do the task. We argue that by interleaving with the well learned visual saccade task initially, and by progressively increasing demand of targeting accuracy from the initial inaccurate behavior, we are shaping the accuracy of the subject's performance for spatial localization, and not that we have trained into the subjects an errant behavior that we interpret as a spatial distortion. Finally, we also point out that the human subjects were instructed to perform the task as accurately as possible but received no feedback of their targeting performance (there was no reward at the end of a trail which depended on targeting accuracy). Since the human performance was similar to that for the monkeys, we assume that the behavior we have measured for both species reflects a distortion in the spatial representation and not a peculiar training effect. A recent paper by Funahashi et al. (1989) present data on monkeys using this task. While they did not analyze the spatial accuracy quantitatively, it appears that the performance was intermediate to our least accurate monkey (using permissive training criteria) and our most accurate monkey (which received feedback on every trial). Presumably, their final training criteria were more stringent than those used for our monkey M88. Moreover, these authors do not specify whether the movements were made in complete darkness, a factor which we show here can effect targeting accuracy.

Becker and Fuchs (1969) were the first to study eye movements made to remembered targets. In their study of human eye movements, they reported that saccades to remembered targets were slower and of longer duration. This finding has been substantiated by others in monkeys (White & Sparks, 1986), as well as reported here. For both types of movements, some of Becher's and Fuch's subjects exhibited a corrective saccade (to an incorrect location), despite the fact that no visual information was available to guide the "corrective" saccade. The stereotyped nature of the movements suggested to them that the planning of the sequence of eye movements was "prepackaged". While our subjects did make some subsequent movements following their primary targeting saccade, most of these additional movements were of relatively long latency (>200 msec) and were not clearly systematic. It is possible to be certain that a secondary saccade were part of a single, initial motor plan only if its latency were shorter than normal saccade latency (~ 200 msec). Otherwise the secondary saccades could be a refixation based on new visual or eye position information at the end of the primary saccade. Based on analysis of the data for 15 deg saccades, we found the incidence of secondary saccades with latencies of 200 msec or less were relatively rare, especially for the monkeys. For the monkeys, they were 1% or less for both remembered saccades and visual saccades. Refixations with latencies less than 400 msec were more common for the visual saccades, with a frequency of about 50%. For the humans, the incidence of short latency (<200 msec) saccades was more frequent and idiosyncratic for both the subject and the direction of movement. In the case of visually guided saccades, they were as high as 20% for one human. Frequency of secondary saccades less than 400 msec latency were as high as 65%. We felt, however, that confining our analysis to the primary saccades served our purpose of measuring the output of the sensorimotor transformation as directly as possible with a convenient and uncontaminated measure of motor performance. Any systematic bias this measure may have introduced into our analysis would seem small due to the relatively infrequent occurrence of short latency (<200 msec) saccades and to the relatively small magnitude (generally less than 1.5 deg error for a 15 deg movement). In comparison to the data of Becker and Fuchs (1969), we can comment that the incidence of short latency corrective saccades was higher in our human subjects than the monkeys. This could be due to species differences or to differences in training. The monkeys were highly trained over a period of months to a very stereotyped set of behaviors. The human subjects, however, were essentially untrained and simply were attempting to perform their interpretation of the instructions. They often exhibited drifting or searching behavior following the primary saccades. Since our analysis compared the same movements (without corrective saccades) to visual targets vs those to remembered targets, we feel it is reasonable that we are investigating the difference in eye movements unique to the remembered saccade task. Additionally, their data do not contradict ours that the incorrect end point of the movements in both cases may be due to a distorted representation of spatial parameters. Furthermore, the movements studied by Becker and Fuchs (1969) were only along the horizontal meridian. We have shown here that the movement trajectories and incidence of secondary saccades for different directions of movement can vary considerably.

Becker and Fuchs (1969) also reported that the slowness of the movements to remembered targets became apparent after about 100–350 msec of memory contingent delay and nearly plateaued after about 1100 msec. Our data concerning the accumulation of spatial distortion follows a similar time couse. We found that the distortion began to accumulate within 100 msec, reached 80% of its maximum value by 800 msec and had nearly asymptoped by 1500 msec. Using a task of fixation of a remembered target, Skavenski and Steinman (1970) and Skavenski (1971) also noted that spatial accuracy remained relatively stable for up to several minutes after the initial error, which accumulated quickly within the first few seconds. Their data did not resolve the time course of accumulation into the sub-second range. This was true even if multiple, deliberate eye movements intervened. This might seem paradoxical, since Hansen and Skavenski (1977, 1985) have shown that highly accurate eye position information seems to be available for somatic motor control, especially during the first 500 msec of memory contingent delay and during saccades (Hansen & Skavenski, 1985). However, it has been argued by several investigators (Hansen & Skavenski, 1985; Matin, Pearce, Matin & Kibler, 1966) that the spatial inaccuracy of eye position control and perceptual spatial localization may be due to poor memory of remembered target location. That is, that eye position is accurately controlled and perceived, but that the spatial inaccuracy may be due to a poor memory of spatial location.

The nature of the temporal accumulation of the spatial distortions suggests that the representation of the target information from a visually-linked to a memory-linked process occurs during the first 800–1000 msec following the offset of the visual target, and after that the representation remains relatively stable. Similarly, Becker and Fuchs estimated that a "visual position error signal" must be available for about 350 msec to elicit saccades of normal velocity (Becker & Fuchs, 1969). It is likely that this time course corresponds to the transformation from the visually-based spatial information to the memory-based spatial representation. Once the transformation has completed, the spatial accuracy of the eye movements remains relatively stable. In the transformation, the spatial information appears to become more noisy (increased variability of targeting) and appears to accumulate a directional bias. The fact that these two phenomena follow the same time course suggests that they are occurring in parallel as part of the same process.

Two additional methodological issues merit special consideration here. First, it should be pointed out here that the relatively large errors in saccade end positions cannot be accounted for by errors associated with the use of a tangent screen for the presentation of the targets. Care has been taken to analyze data from movements where the ocular divergence demands were symmetrical. Furthermore, the change in eye position associated with divergence for targets out to 40 deg eccentricity is only about 0.5 deg. The observed targeting errors were much larger than this, on the order of about 3 deg average for the monkeys and about 1.5 deg for the humans. Since we measured the position of only one eye, we make the assumption in these studies that this represents the conjugate direction of gaze. It is possible that in the dark, the subjects may have converged or diverged to positions inappropriate for the true depth of target. However, previous studies in humans using a similar task have shown that this error in the disconjugate domain is small (Bracewell, Husain & Stein, 1991). Furthermore, the use of the 50 deg/sec cutoff for the end of the saccade would tend to exclude most vergence movements, especially the slower movements made in the dark. Finally, since the targeting errors have been measured compared to movements made to visual targets, any error represents inaccuracy of the visual-motor performance unique to the memory related task, regardless of whether it had occurred in the conjugate or vergence domain.

Second, the method we have used to determine targeting error does not measure the error of the movements from the absolute target position, since the saccades to visual targets may not have acquired the targets exactly. Instead, we have determined the differences in oculomotor performance by measuring the end positions of the remembered saccades relative to those for visual saccades. We chose this method to measure directly the difference in the output of the sensorimotor spatial transformation for the memory-linked task. However, since the visually guided movements generally fell to within an error of less than 10% of the distance to the targets (especially for the highly trained monkeys), these numbers do not vary greatly from the spatial distortions one would measure from target position.

Experimental investigations in monkeys provides us with relevant neurophysiological data concerning primate visual and oculomotor processes and allows some speculation about the biological basis of these findings. For making saccades to visible targets, direct visual input from cells in the primary visual pathway and extrastriate visual areas is available to the oculomotor control system. These neurons provide faithful information about the spatial location of the target with a high degree of accuracy. For making saccades to remembered targets, the target location is dependent on a memory-linked representation of space without the benefit of input from the spatial accuracy inherent in the visual system. Mays and Sparks (1980b) described cells in the deep layers of the superior colliculus which were shown to carry information about desired change in eye position (motor error) during sequences of two eye movements where parameters of the motor planning sequence had to be based on memory of previously seen visual targets. These cells were termed "quasi-visual" cells because they responded to visual stimuli, but did not require a visual stimulus to fall within their response field. More recent studies by White and Sparks (personal communication) have shown that these cells can hold their memory-related signal of motor error for several seconds when planned eye movements are withheld during forced delays between stimulus presentation and movement to the target. Similar activity has been reported within the intraparietal sulcus of posterior parietal cortex (area LIP) and was interpreted as a memory-related motor-planning signal of intended change in eye position (Gnadt & Andersen, 1988). Furthermore, sustained neuronal activity during eye movements to remembered visual targets has been reported in the frontal eye fields and dorsomedial prefrontal cortex (Bruce & Goldberg, 1985; Funahashi et al., 1989). The coordinate frame used by these frontal cortical cells has not been established.

Presumably these neurons are involved in the memory-linked sensorimotor transformation process. Significantly, the three cortical areas are all reciprocally interconnected and also interconnected with the area 7a (Andersen, Asanuma & Cowan, 1985a; Andersen, Essick & Siegel, 1985b; Petrides & Pandya, 1984; Blatt, Stoner & Andersen, 1987) where the specific retinotopic to craniotopic transformation has been documented (Andersen et al., 1985). Additionally, area LIP and the frontal eye fields both project to the superior colliculus (Lynch, Graybiel & Lobeck, 1985; Fries, 1984; Asanuma, Andersen & Cowan, 1986). One salient feature of the responses of all of these neurons are that they are broadly tuned for the spatial parameters to which they are responsive. In other words, during relevant visual-motor behaviors each neuron participates in a relatively broad, though restricted, range of visual stimulus and/or oculomotor spatial parameters. Information about the specific, finely tuned, spatial parameters is contained in the unique subset of neurons which are active for a given spatial location. One possible explanation for the behavioral results described here can be found in the nature of this form of spatial representation. Accuracy for this type of distributed information is dependent on the participation of numerous elements within the neuronal pool, since the information carried by any given cell is ambiguous. Computational models of this form of information coding scheme have been shown to have numerous nonlinear elements (Goodman & Andersen, 1989). Significant reduction in the number of active units within the relevant neuron pool would produce a loss of spatial information accuracy, and nonlinear shifts in neuronal pool output could result from the interaction of which particular cells within the network tended to respond and which did not. Rohrer et al. (1987) have shown that many cells in the superior colliculus active during movements to visual targets are not active in the memory related task. This seems to be true in parietal cortex as well (Gnadt & Andersen, unpublished observations). Thus, it is possible that such a distributed nature of the visual-motor transformation process could account for the nonuniformity of the spatial distortion for the different directions of eye movements. It remains to be determined whether this form of spatial coding scheme is utilized by the brain to perform this task.

Furthermore, we would suggest that, at least in part, the reduced velocities of the saccades to remembered targets may be due to reduced content of information about target end position from higher motor control centers. Visual spatial information in higher centers is coded as neuronal maps (e.g. superior colliculus, frontal eye fields, posterior parietal cortex) where the specific subset of active neurons defines the spatial location. This spatial code must be transformed into a temporal code of eye position such as found at the ocular motor neurons. Reduced information input from these higher centers may transpose into reduced temporal output at the final motor output during the sensorimotor transformation. Specifically, Lee, Rohrer and Sparks (1988) have proposed that the superior colliculus is involved in this spatial to temporal transformation and it has been documented that experimental reduction in the number of active superior colliculus cells during saccades produces slower velocity saccades (Hikosaka & Wurtz, 1986; Lee et al., 1988).

In summary, we describe here a memory related process of spatial localization as measured by the end position of eye movements made to acquire the remembered target locations.

(1) The memory related eye movement task requires a spatial transformation process which has an inherently less precise spatial resolution. The transformation accumulates error in both mean position (constant error) and in trial-to-trial variance (variable error).

(2) The process does not retain accurate retinotopic registration. The error is nonuniform for the direction and eccentricity of the target from the initial point of fixation. While some overall upward shift in mean spatial distortion was apparent (especially in the monkeys), this shift was not uniform. This distortion can be described as a retinotopic spatial map, plus a nonrandom directional error having a directional but nonlinear bias, plus a random directional error.

(3) Factors related to initial eye position and head position can effect the movement, suggesting that the sensorimotor transformation utilizes a frame of reference that is not oculocentric.

(4) The majority of the process occurs during the first 800 msec of memory-dependent delay of the eye movement, rising more slowly after that.

(5) The nonrandom directional distortions in mean end position error and the random trial-to-trial variance in error follow the same time course and are probably a manifestation of the same process.

(6) The process is plastic and improves with training.

(7) The presence or absence of visual cues directly related to the target itself seems to be critically important to the spatial localization accuracy and the dynamic performance of the memory-linked eye movement task.

(8) The process also parallels changes in the temporal properties of the eye movements. Since the temporal parameters of eye movements are derived from information coded spatially (e.g. the spatio-temporal transformation from the superior colliculus to the pontine saccade generator), these temporal abnormalities may be a consequence of the reduced spatial information content in the sensorimotor transformation.

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