

D.Y.P. Henriques · J.D. Crawford

Direction-dependent distortions of retinocentric space in the visuomotor transformation for pointing

Received: 8 April 1999 / Accepted: 17 December 1999 / Published online: 25 March 2000
© Springer-Verlag 2000

Abstract The aim of this study was to: (1) quantify errors in open-loop pointing toward a spatially central (but retinally peripheral) visual target with gaze maintained in various eccentric horizontal, vertical, and oblique directions; and (2) determine the computational source of these errors. Eye and arm orientations were measured with the use of search coils while six head-fixed subjects looked and pointed toward remembered targets in complete darkness. On average, subjects made small exaggerations in both the vertical and horizontal components of retinal displacement (tending to overshoot the target relative to current gaze), but individual subjects showed considerable variations in this pattern. Moreover, pointing errors for oblique retinal targets were only partially predictable from errors for the cardinal directions, suggesting that most of these errors did not arise within independent vertical and horizontal coordinate channels. The remaining variance was related to nonhomogeneous, direction-dependent distortions in reading out the magnitudes and directions of retinal displacement. The largest and most consistent nonhomogeneities occurred as discontinuities between adjacent points across the vertical meridian of retinotopic space, perhaps related to the break between the representations of space in the left and right cortices. These findings are consistent with the hypothesis that at least some of these visuomotor distortions are due to miscalibrations in quasi-independent visuomotor readout mechanisms for “patches” of retino-

topic space, with major discontinuities existing between patches at certain anatomic and/or physiological borders.

Key words Pointing · Visuomotor · Eye position · Calibration · Spatial vision · Human

Introduction

The direction and magnitude of visual target locations are initially encoded with respect to current gaze direction by the site of retinal stimulation. This form of representation is maintained, with certain well-known distortions, in the retinotopic and quasi-retinotopic maps of the occipital lobe, superior colliculus, posterior parietal cortex, premotor cortex, and prefrontal cortex (Funahashi et al. 1990; Goldberg and Bruce 1990; Munoz et al. 1991; Waitzman et al. 1991; Moschovakis and Highstein 1994; Schall 1995). Recent experiments have suggested that intended and remembered targets for goal-directed arm movements are also encoded in a retinal frame (Henriques et al. 1998; Batista et al. 1999). However, the internal representation of stimulus location must thereafter be transformed into coordinates appropriate for muscular contraction (Soechting and Flanders 1989a, 1989b; Gnadt et al. 1991; Caminiti et al. 1998; Henriques et al. 1998). Thus, the accuracy of the motor output depends critically on the calibration of this visuomotor transformation on a moment-to-moment and day-to-day basis (Ghilardi et al. 1995; Imamizu et al. 1995; Vetter et al. 1999). Conversely, consistent errors in the accuracy of visually guided movements due to imperfect calibration may sometimes provide clues into the neural algorithms for such transformations (Soechting and Flanders 1989a, 1989b; Flanders et al. 1992; Caminiti et al. 1996; McIntyre et al. 1997).

For example, when pointing (open loop) toward visual targets, subjects tend to exaggerate the horizontal retinal eccentricity of nonfoveal stimuli (Bock 1986, 1993; Enright 1995; Henriques et al. 1998). When both target direction and fixation direction are independently varied,

D.Y.P. Henriques · J.D. Crawford
Centre for Vision Research,
MRC group for Action and Perception, York University, Toronto,
Ontario, Canada, M3J 1P3

D.Y.P. Henriques · J.D. Crawford (✉)
Department of Psychology, York University, 4700 Keele Street,
Toronto, Ontario, Canada, M3J 1P3
e-mail: JDC@yorku.ca
Tel: +1-416-7365121, Fax: +1-416-7365814

J.D. Crawford
Department of Biology, York University, Toronto, Ontario,
Canada, M3J 1P3

the resulting pattern of pointing errors suggests that this effect is indeed a misinterpretation of target location in a retinal frame (Bock 1986; Henriques et al. 1998), rather than an eye position effect as previously believed (Morgan 1978; Hill 1972). This is consistent with recent findings that the visuomotor transformation for pointing is most easily calibrated in an eye-centered frame (Vetter et al. 1999). Moreover, in terms of percentage, the retinal exaggeration effect is remarkably strong at small retinal eccentricities, but tends to saturate at approximately 15° . This effect has a number of practical implications for human performance (Henriques et al. 1998) and is potentially problematic for pointing studies that do not control for gaze direction (Adamovich et al. 1988; Vindras et al. 1998; Gentilucci and Negrotti 1994; McIntyre et al. 1997). However, its overall pattern in two-dimensional (2-D) retinal space and underlying origin remain somewhat obscure. Previous studies have described a similar effect for oblique and vertical targets (Enright 1995), but these studies tended to hold gaze constant and vary pointing direction, which might have potentially confounded the “retinal exaggeration” effect with control system errors related to purely motor aspects of pointing in different directions (Bock 1986, 1993; Enright 1995).

The first goal of this study was to thoroughly describe and quantify the pattern of these retinotopic distortions in two dimensions with the use of a paradigm in which the motion requirement of the task remained invariant. Pointing behavior provides a good measure for assessing these distortions, since it agrees well with verbal accounts of perceived target direction (Gauthier et al. 1990). In contrast to previous studies of vertical and oblique retinal displacements (Bock 1993; Enright 1995), our aim was to isolate the retinal exaggeration effect by varying gaze direction and requiring subjects to point toward a consistent remembered target direction. Whereas our earlier study only reported visuomotor distortions of horizontal retinal displacement (Henriques et al. 1998), the current study comparatively describes the effect for vertical, oblique, and horizontal retinal displacements. Furthermore, whereas previous studies focused on the gain of retinal exaggeration, we also quantified both the magnitude and the direction of pointing errors as a function of retinal displacement direction. The latter is of particular interest in light of recent evidence that the preferred tuning direction of some cortical arm movement neurons changes when gaze and pointing direction are disassociated (Caminiti et al. 1998), as is the case in the current study.

The second goal of this study was to determine the computational stage of neural processing in which this effect might originate. Presumably this exaggeration effect occurs because it is one that does not normally obtain the visual feedback necessary for sensorimotor calibration when pointing toward nonfoveal targets (Henriques et al. 1998). However, this does not comment on the neural calibration algorithm involved. Although it is tempting to think that these gaze-centered pointing errors imply that distortions exist within the retinocentric maps

of the cortex themselves, this idea is misleading, because the spatial content of any one point on a retinotopic map is only given meaning by the way that it is mapped onto (through functional neural connections) a pattern of muscular contraction. What can the gaze-centered pattern of pointing errors tell us about this process?

However, one possibility is that these miscalibrations occur as a global offset relative to some fixed egocentric frame (Vetter et al. 1999), but this would not account for the saturating effects that have already been reported (Bock 1986, 1993; Henriques et al. 1998). A number of studies have suggested that visuomotor transformations employ an intermediate stage that parcels visuomotor space into separate vertical and horizontal coordinates (Soechting and Flanders 1989a, 1989b; Masino and Knudsen 1993; Crawford 1994). If the retinal miscalibration effect were due to saturating gain errors within two such coordinate axes in a retinal frame, the horizontal and vertical components of these errors should sum independently (i.e., with minimal interaction) when localizing oblique targets (Bedford 1989, 1993, 1994).

Alternatively, these visual miscalibrations could occur in the process of separate “readout” mechanisms for separate points on the retinotopic map, which does not in itself utilize a coordinate system, but rather occurs at different sites for each different target location. For example, in studies where small areas of the “visuomotor map” for pointing were intentionally “decalibrated,” the resulting errors generalized strongly to local points in the work space, but only weakly for more distant sites (Ghilardi et al. 1995; Ghahramani et al. 1996). This suggests a calibration mechanism specific to relatively local readouts of individual sites on a topographic map, which could result in site-specific retinal inhomogeneities (Miller 1996; Bockisch and Miller 1999). If the retinal exaggeration effect were due to errors in this type of mechanism, its magnitude and direction could potentially vary randomly and discontinuously across retinotopic space, with considerable variability between subjects.

Finally, an intermediate scheme could also be possible, where errors across particular patches of visual space show a tendency to generalize quasi-homogeneously, with sharper discontinuities at certain borders that might correspond to anatomic borders in physiological representation (Martin et al. 1996; Ghahramani and Wolpert 1997). If so, then some of these discontinuities should be common across subjects. We tested between these possibilities by: (1) measuring the degree of interaction between vertical and horizontal errors to oblique targets; and (2) evaluating the continuity of both the magnitudes and directions of the effect across visual space, with particular care to distinguish between idiosyncratic individual patterns and the trends across subjects. Some of the results have been reported in abstract form (Henriques and Crawford 1998).

Materials and methods

Subjects

Six right-handed human subjects (four women and two men, aged 24–43 years) with no known neuromuscular deficits participated in the experiment. Three subjects had normal acuity without correction, while the remaining subjects wore their usual corrective lenses during the experiment. This was done to ensure that subjects were in their normal state of optical calibration. Two of the subjects, J.C. and D.H., were aware of the nature and design of the experiment, while the rest were na. There were no apparent differences in overall pointing performances between the na and informed participants. All experimental procedures were approved by York Human Participants Review Subcommittee. Informed consent was obtained from all the subjects.

Apparatus

The orientation of the right eye and right arm were measured using the three-dimensional (3-D) magnetic field scleral search-coil technique (Tweed et al. 1990; Henriques et al. 1998). Each subject was seated with their right eye at the center of three mutually orthogonal pairs of Helmholtz coils, 2 m in diameter. The subject's head was mechanically stabilized, in the upright position, with the use of a personalized bite bar attached to the experimental chair. The subject's right arm rested on the arm of the chair between trials. Skalar (Delft, The Netherlands) 2-D eye coils were placed in the anesthetized right eye of each subject. A "home-made" dual 3-D search coil embedded in plastic was secured to the lateral surface of the upper arm such that the search coil was centrally located within the Helmholtz coils during pointing. Note that the precise position of this coil on the upper arm was irrelevant to com-

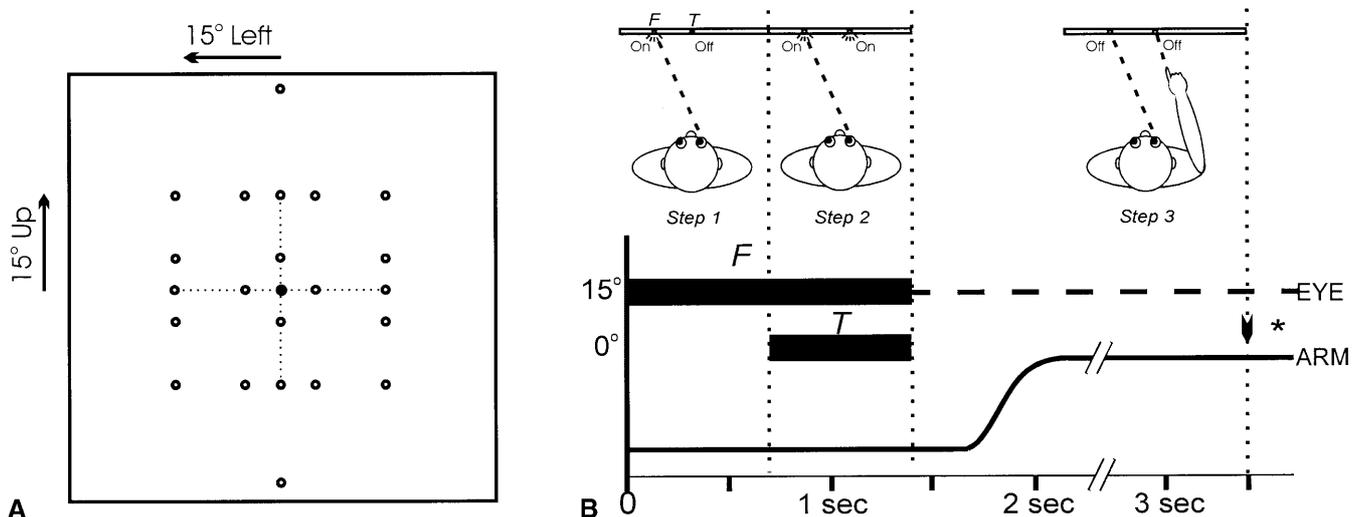
puting its relative orientation. With the arm straight during pointing, the overall rotation of the arm could be effectively measured. The data were sampled by a PC at a rate of 50 Hz.

The stimuli consisted of light-emitting diodes (LEDs, 0.17° in diameter and 2.0 cd/m^2 luminance) placed on a black tangent screen that was positioned 110 cm from the subject's eyes. The experimental chair was adjusted vertically such that the central LED was at the same elevation as the right eye. The interocular axis was measured to confirm that the subject's head was properly aligned with the stimulus display (mean tilt of $0.11 \pm 1.02^\circ$ SD). The spatial arrangement of the 23 LEDs is shown in Fig. 1A (empty circles). Eight of these LEDs were positioned eccentrically at 5° and 15° to the left and right, above and below the central LED, as well as an additional two LEDs vertically displaced from center by 30° . We defined these as "cardinal" LEDs, since they were displaced (re: the center) in only one of two dimensions. Another 4 of the LEDs were placed at an angle of 45° off-axis, with a horizontal and vertical displacement of 15° , which we refer to as the "standard" oblique LEDs. The final 8 LEDs were also oblique, with either a 15° horizontal or vertical component and a 5° component in the orthogonal direction. These are referred as "horizontally dominant" and "vertically dominant" oblique LEDs, respectively. The duration of illumination of each LED was also recorded.

Procedure

In our standard task, the central LED was used consistently as the pointing target to reduce any variation due to possible motor effects associated with increasing displacements of the arm (Bock and Eckmiller 1986). Subjects were asked to point as accurately as possible toward the central target (T) with their index finger and their arm fully extended, while maintaining fixation toward one of the selected 22 LEDs (fixation point, F). The basic paradigm is shown in Fig. 1B, where it is broken down into three steps, depicted by the cartoon, while the schematic horizontal trajectory of the eye (dashed line) and arm (solid line), and LED illumination (black rectangles) are plotted against time. The typical trial began with subjects looking continuously at F (e.g., 15° left) for 1.4 s (step 1). After 0.7 s, T was illuminated for 0.7 s (step 2) before both LEDs were extinguished (step 3). In total darkness, the subjects were then required to point immediately to the remembered location of T , while maintaining gaze fixed in the direction of F (step 3). The arrow (Fig. 1B) indicates the approximate time when final pointing and fixation directions were selected. An auditory tone signaled the subjects to lower their arm back to their resting positions and prepare for the next trial. This paradigm was repeated for all experimental conditions for the various Fs.

Fig. 1A,B The experimental paradigm. **A** The arrangement of the pointing target LED (*center*) and fixation LED sites (*empty circles*) on the screen. **B** Horizontal eye (*dashed line*) and arm position (*solid line*) are plotted, with accompanying depiction of the task against time. *Thick black boxes* indicate the location and duration of the pointing target (T) and fixation (F) LEDs. Subjects were required to look continuously at F (*Step 1*); after 0.7 s, T was illuminated (*Step 2*) and then, after another 0.7 s, both LEDs were extinguished. Subjects were then required to point toward the remembered location of T while continuing to look toward F (*Step 3*). *Arrow*, approximate time of selection for final pointing direction. An auditory tone (*asterisk*) indicated the end of each trial and signaled the subject to return to the resting position



The control pointing task, where subjects both fixated and pointed toward the central target ($F=T$), was included in all conditions as a control. In addition, some trials employed a randomly selected eccentric T (displaced 5° in any one of the cardinal directions), rather than the standard T , to ensure that subjects were actively attending to the visual pointing target and not merely making stereotypical, proprioceptively guided movements toward the central direction. These nonstandard target trials were not included in the data analysis.

Subjects were required to practice all three experimental conditions for ≈ 15 min on the day prior to the experiment, without receiving any visual or verbal feedback on their performance. This was done to familiarize the subjects with the task and to avoid confusion during the experiment. In the first experimental condition, the vertical series, each subject pointed five times to the central target while looking toward each of a series of seven F s: 30° up, 15° up, 5° up, 0° (control pointing task), 5° down, 15° down, then 30° down. This condition was designed to emulate the serial fixation directions used in our previous study that manipulated horizontal retinal displacements (Henriques et al. 1998). The presentation of the fixation LEDs was ordered from top to bottom so that if subjects made pointing errors in the opposite direction, as predicted (Henriques et al. 1998), this could not be interpreted as fatigue. For the second *cardinal* condition, pointing tasks for F were placed 15° and 5° up, down, left, and right relative to the center. These targets were presented randomly in five consecutive blocks. Each block included a trial for each of the eight cardinal F s, as well as two control pointing tasks and one nonstandard target trial, for a total of 55 (11×5) trials per condition. The third oblique condition used a total of 12 oblique F s: four standard obliques, four vertically dominant obliques, and four horizontally dominant obliques. These 12 F s were randomly presented within each of five consecutive blocks, with each block including two control pointing tasks and one nonstandard target trial, for a total of 65 trials. The cardinal and oblique conditions were repeated twice for a total of ten data points in each fixation direction.

For simplicity, “cardinal pointing errors” and “oblique pointing errors” here mean errors in pointing during fixations in the cardinal and oblique directions (i.e., cardinal and oblique retinal displacements), respectively. Since we were interested in examining pointing accuracy (rather than precision) as a function of retinal displacement, we primarily considered mean pointing errors in the current paper. The term “retinal displacement” refers to the stored representation of the target in retinal coordinates. It was computed via the standard practice of subtracting the 2-D eye position vector from target position, which amounts here to the reverse of fixation direction relative to the target, since the target is always at zero. Calculation of retinal displacement is more complex for other eye position and target configurations (Crawford and Guitton 1997; Klier and Crawford 1998). However, since the target was maintained at the center of the oculomotor map in the current study, this estimation of retinal displacement was sufficient here.

Accurate pointing toward nonstandard targets was confirmed off-line. The remainder of the experiment consisted of calibration tasks. One of these tasks required the subjects to fixate and point toward the illuminated T for 10 s, with feedback, in order to compute a reference position from which all other arm positions were described. The remaining tasks required the subjects to rotate their eyes, head, and arm as far as comfortably possible (after removing the bite bar) along the horizontal (pitch), vertical (yaw), and torsional (roll) axes, for the purposes of signal calibration (Henriques et al. 1998; Klier and Crawford 1998).

Data analysis

The details of our calibration and data analysis techniques have been reported previously (Tweed et al. 1990; Hore et al. 1992; Henriques et al. 1998). For the purpose of display, *ocular* coil signals were treated as 2-D “gaze vectors,” but they were further converted into angular measures of azimuth and elevation for statistical analysis. Arm coil signals were first converted into quatern-

ions, where each final arm position was described as a rotation vector from the initial reference position. Arm quaternions were also converted into 2-D pointing directions (for graphic designs), as described previously (Tweed et al. 1990; Henriques et al. 1998), and then into angular measures of position for quantitative analysis. Since the arm was fully extended during pointing, this measure completely specified the 2-D pointing direction of the arm relative to the subjectively chosen ideal pointing direction toward T . This method allowed us to compute relative pointing errors with the arm extended without a more complex and unnecessary depiction of multijoint arm position.

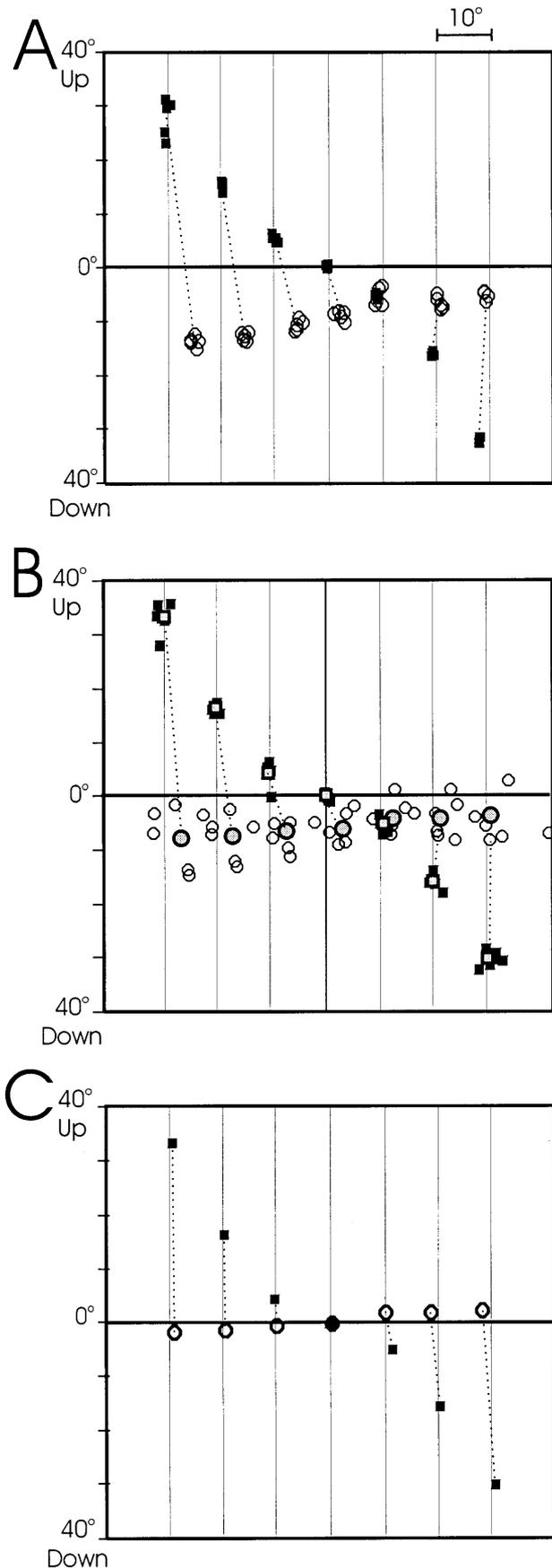
The trajectories and temporal sequencing of eye and arm movements were similar to those illustrated in our previous report (Henriques et al. 1998), so only final positions of the eye and arm during pointing were analyzed. These positions were selected visually at the point where the arm reached its final position and maintained stability, for trials where subjects correctly moved their eyes and arm according to the requirements of the paradigm (more than 90% of trials). Statistical analysis (pairwise t -tests and repeated-measures one-way ANOVAs) was performed with the SPSS statistical package.

Results

Pointing results for a consecutive series of vertical fixation directions

Figure 2 shows 2-D pointing performance toward the central target, while subjects maintained gaze toward a series of seven vertically eccentric directions (vertical series condition). Figure 2A shows all five pointing trials (empty circles) for each of the seven fixation directions (filled squares) for one typical subject, with the ordinate axes sequentially shifted horizontally for each pointing target to avoid overlap. The site of the desired central pointing target is denoted by the intersection of the abscissa with each shifted ordinate. Dashed lines in Fig. 2A join the corresponding sets of fixation and pointing data. The subject tended to miss the target consistently in the downward direction for all the vertical fixation directions (the “vertical offset”). The pointing response was also gaze direction-dependent. In this particular case, the subject tended to miss to the right for upward fixation directions but not for downward fixations. Moreover, note that pointing direction tended to rise as gaze was lowered (progressing left to right in Fig. 2A). In contrast, the trial-to-trial pointing precision for a given fixation direction was quite high. Averaged across targets and then across subjects, the cross-trial SD of pointing direction was only 0.92° (horizontal angle) and 1.21° (vertical angle).

Figure 2B shows a similar plot of the cross-trial means for each and every subject and the averaged results across subjects (gray symbols). For any one fixation direction, there was considerable variation in pointing direction across subjects, particularly in the vertical direction (mean SD across subjects, 3.38°), and at greater fixation eccentricities. However, all subjects showed both a downward bias and some form of gaze-direction dependence of pointing responses. When gaze direction was maintained at center, pointing responses were, on average, shifted downward by 6.19° and rightward by



3.32° relative to the target. The horizontal error tended to increase as gaze stepped up and decrease as gaze stepped down. On average, pointing direction rose as gaze went down for most subjects such that the vertical undershoot, relative to the target, tended to decrease as final eye orientation moved from 30° up (mean pointing error 7.78°) to 30° down (mean pointing error 3.71°). Although pointing errors were small overall, statistical analysis (repeated-measures ANOVA) showed that the mean pointing results, across subjects, between the zero, upward, and downward retinal displacements were significantly different ($P \leq 0.024$). However, this trend was partially obscured by the constant vertical offset, which was unrelated to gaze direction.

In order to better examine the pattern of localization errors as a function of retinal displacement and to reduce any overall bias that is not related to gaze direction, we shifted the pointing data to correct for the constant pointing errors that arose when subjects fixated the central target (control). The corrected data are shown in Fig. 2C (i.e., raw errors minus control errors). With this convention, the dependence of mean pointing errors on retinal displacement was more readily apparent, with the mean pointing response shifting upward (and leftward) as gaze direction stepped downward. Once shifted in this manner, this pattern qualitatively resembled the pattern of pointing errors that we reported previously for a similar horizontal fixation paradigm (Henriques et al. 1998). Since we intended to examine the pattern of visuomotor miscalibrations as a function of retinal displacement, we henceforth exclusively examined pointing performance relative to control pointing with each paradigm in this fashion.

Since the latter dependence of vertical pointing direction on vertical gaze direction was similar to the retinal exaggeration effect described for horizontal target displacements, we chose to quantify this aspect of the data in more detail in order to compare it with the analogous horizontal results. Figure 3 shows mean vertical pointing errors relative to controls (expanded for clarity), plotted as a function of vertical fixation direction. Figure 3A shows the mean error functions for individual subjects, denoted by symbols joined by dashed lines. In order to reduce any overall bias in pointing that might be purely motor in origin, we shifted the individual pointing curves. Again, the trend in most subjects was for pointing direction to ascend as gaze descended, but there was considerable variability between the individual patterns. Only one subject showed the classic saturating retinal exaggeration effect (Bock 1986; Henriques et al. 1998)

Fig. 2A–C Pointing during a series of seven vertical fixation directions. Final 2-D eye orientation (*filled squares*) and pointing responses (*empty circles*) are plotted for each fixation LED (horizontally staggered) for one subject (**A**). Mean responses for each of six subjects and an overall mean (*gray symbols*) are also plotted relative to target (**B**) and relative to mean control pointing (**C**). *Dashed lines* join the corresponding groups of gaze and pointing direction

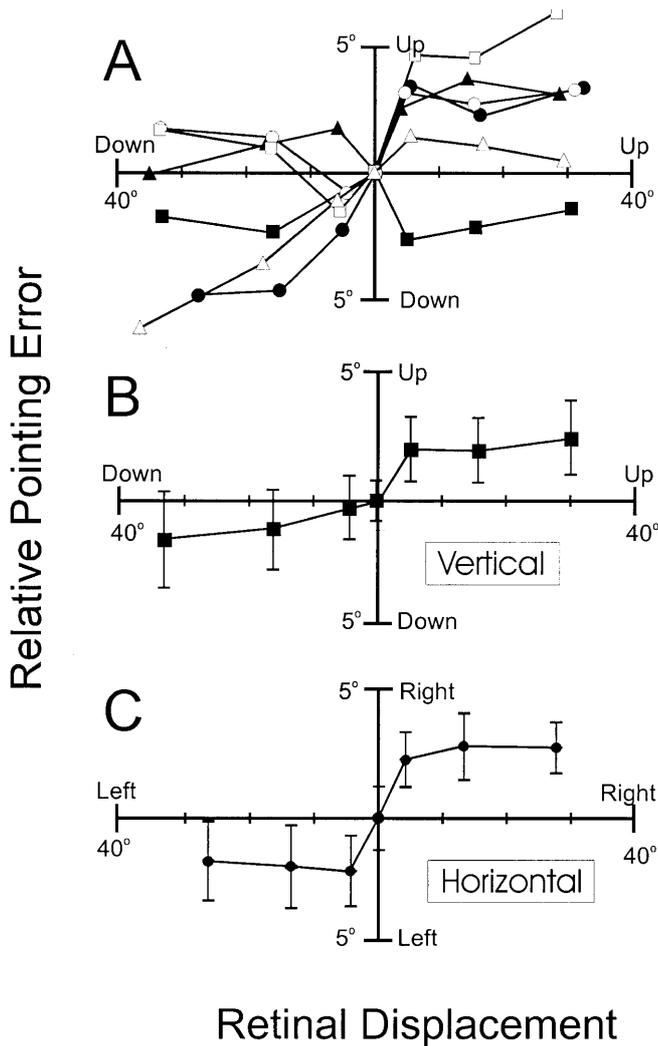


Fig. 3A–C Final vertical pointing errors, relative to controls, plotted (along the expanded ordinate) as a function of vertical angular retinal displacement. **A** Mean results for each subject (*all symbols*). **B** Mean results across subjects (*filled squares*). For comparison, results of a similar task for *horizontal* retinal displacements from a previous study (Henriques et al. 1998) are plotted (**C**). *Vertical lines* indicate standard deviations between means of subjects

for both directions of retinal displacement. Three subjects (empty squares, empty circles, black triangles in Fig. 3A) only showed the reported trend for upward retinal displacements, and one subject (filled squares in Fig. 3A) only showed the effect for downward retinal displacements. Moreover, four of the subjects (empty squares, filled squares, empty circles, black triangles in Fig. 3A) showed relatively sharp reversals in the direction of the effect in the (angular) vicinity of the foveated target. Thus, there was considerable variation of the pattern between subjects.

Nevertheless, when averaged across all subjects, the effect was similar to that reported in previous studies for horizontal retinal displacements. For reference, we compared mean retinal overshoots in the vertical pointing direction (Fig. 3B) with mean retinal overshoots in the

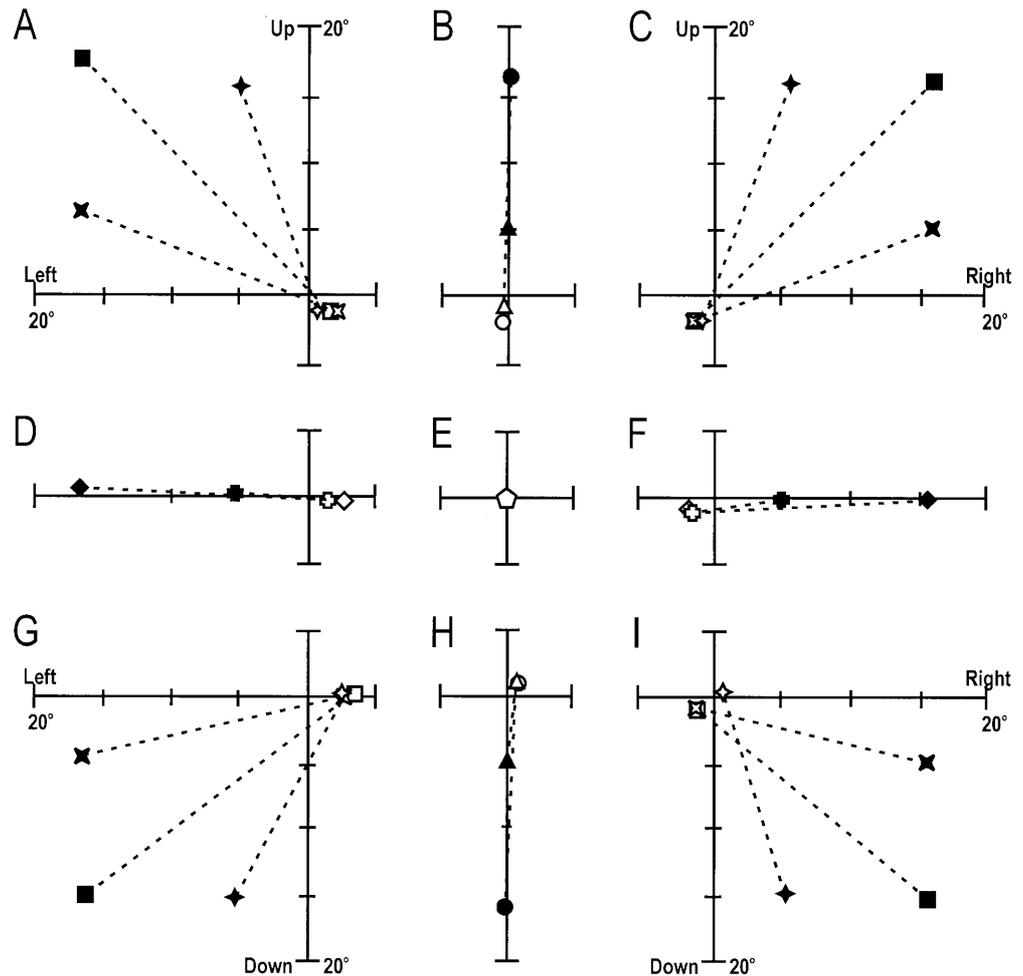
horizontal pointing direction (Fig. 3C), measured in a previous study for a similar task that manipulated horizontal retinal displacement (Henriques et al. 1998). Comparisons between the two show a similar intersubject variance and a similar saturating pattern of pointing errors as a function of retinal displacement, although the effect was somewhat stronger in the horizontal condition. In contrast to most of the individual subjects, the overall trend of dependence in retinal magnitude did not show any pronounced peaks or irregularities.

Pointing performance while randomly fixating in cardinal and oblique directions

Having confirmed that pointing responses during a series of fixation displacements along the vertical dimension were gaze dependent and showed similar trends to a similar paradigm along the horizontal dimension (Henriques et al. 1998), we next analyzed the influence of gaze direction on pointing accuracy during the randomized 2-D task. We first considered the general trends. Figure 4 shows mean (averaged within and then across subjects) 2-D pointing results (open symbols) joined by dashed lines to corresponding 2-D fixation directions (closed symbols), plotted in space coordinates. For simplification and to reduce overlap, the results for the 21 fixation targets are segregated into nine panels in Fig. 4, arranged in relative spatial register with the fixation LEDs. Note that pointing responses were shifted relative to mean control pointing (which again was in the left and downward directions for most subjects), such that pointing to the central target (Fig. 4E) was perfectly accurate by default. Therefore, the intersection (origin) of the two axes for each panel represents the pointing direction during central fixation (rather than target direction), and the open symbols designate pointing errors relative to these controls.

In general, pointing errors relative to controls were small. Nonetheless, the mean pointing responses tended to overshoot the target relative to gaze direction, i.e., in the direction of retinal target displacement, as in the previous paradigm. Pointing performance during fixations in the four cardinal directions is shown in Fig. 4B,D,F,H. As was observed in the vertical series paradigm, vertical pointing errors during both upward, downward, and central fixation were significantly different from each other ($P \leq 0.001$, one-way repeated-measures ANOVA). Similarly, horizontal localization errors, when gaze was maintained to the left, right, and on center during pointing, were also significantly different ($P \leq 0.001$, one-way repeated-measures ANOVA). During vertically eccentric fixation, the retinal exaggeration, expressed as the magnitude of vertical pointing error divided by retinal displacement as a percentage, was 14.63% (mean across subjects, $\pm 5.38\%$ SD). This was slightly, but significantly smaller than the percentage of horizontal exaggerations during horizontal fixation, 21.71% ($\pm 4.20\%$ SD; $P \leq 0.016$ pairwise *t*-test), in the same paradigm.

Fig. 4A–I Two-dimensional mean pointing responses (*empty symbols*) for cardinal and oblique fixation directions (*filled symbols*) plotted in space coordinates and divided into nine panels (A–I). Note that pointing results are plotted relative to control pointing (E). *Dashed lines* join the corresponding fixation and pointing directions. Despite different directions, common symbols denote similar *F* displacement from center: 5° horizontal (*filled triangles*); 15° horizontal (*filled circles*); 5° vertical (*filled crosses*); 15° vertical (*filled diamonds*); standard oblique (*filled squares*); horizontally dominant oblique (*skewed stars*); and vertically dominant oblique (*stars*)



Based on this pattern of pointing errors for cardinal horizontal and vertical retinal displacements, we expected that oblique retinal displacements would also produce pointing errors, in the direction opposite to fixation, along both the horizontal and vertical axes. The corners of Fig. 4A,C,G,I show 2-D localization errors when subjects fixated three oblique directions in each of the four panels. For downward, oblique retinal displacements (from the upper LEDs), subjects, on average, exaggerated angular eccentricity in both directions (Fig. 4A,C). For example, when subjects looked up and to the left, they pointed down and to the right of control pointing responses. On average, subjects exaggerated the retinal displacement of the targets by 13.10% ($\pm 14.60\%$ SD) in the horizontal direction and by 6.26% ($\pm 13.79\%$ SD) in the vertical direction.

As described in the Introduction, previous investigations (Bock 1986; Henriques et al. 1998) have conducted controls to show that such pointing errors occur as a function of retinal displacement rather than eye position. However, before proceeding to a more in-depth analysis, we performed an extra control to check whether these pointing errors could be due to a misperception of the pointing target due to a drift in gaze direction during the “LEDs off” phase of pointing (step 3 in Fig. 1B). For example, the eyes

might tend to drift toward center during fixation in the dark, i.e., in the same direction as pointing error. Hypothetically, if the internal representation of the remembered target drifted in the same direction as the eyes, then this could explain some of our results. If this were the cause of these errors, then pointing errors should correlate with gaze drift. To test this, we first measured horizontal and vertical drifts by subtracting the fixation direction while subjects looked at the illuminated fixation LED from the fixation direction subjects maintained at the time the data were sampled during pointing. Second, we plotted errors in pointing direction as a function of these drift scores. The correlation coefficient and slope for each subject are given in Table 1. The mean correlation coefficient and slope were small, with a mean r^2 of 0.083 and 0.065 for the horizontal and vertical drift components, respectively. This poor relationship between drift and pointing errors suggests that pointing errors, in the direction opposite to gaze, were not due to a misestimation of eye position due to ocular drift.

Linear predictability of the 2-D error function

If these pointing errors originated from gain errors in two separate horizontal and vertical “channels,” then the

pointing errors incurred from oblique target displacements should be predictable as the vector sum of the pointing errors produced at the separate corresponding horizontal and vertical components of retinal displacement. For example, the pointing errors from the oblique fixation directions in Fig. 4G should be predictable from the vector sum of the pointing errors in Fig. 4D and H. This behavior would result from the (hypothesized) linear independence of the horizontal and vertical channels

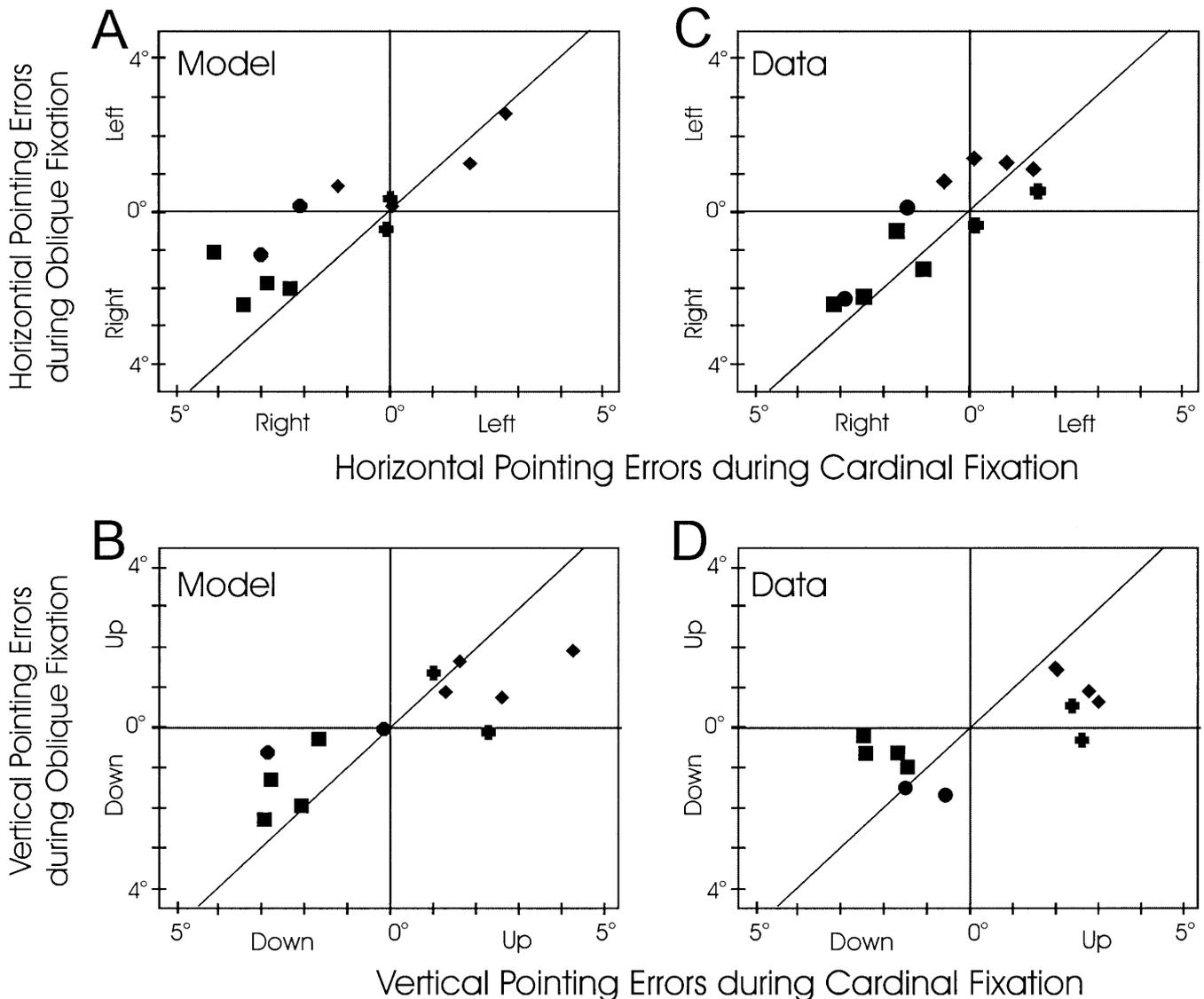
and would not conflict with the nonlinearities within each channel. To test this hypothesis, we plotted mean actual pointing errors for oblique retinal displacements as a function of the vector sum of the pointing errors from the corresponding horizontal and vertical cardinal retinal displacements (Fig. 5). This was reduced to two

Fig. 5A–D Mean horizontal (A,C) and vertical (B,D) pointing results during oblique fixations plotted as a function of the summed vectors of results during cardinal fixations with corresponding displacements for values generated by the overshoot model (A,B) and for one subject, averaged across trials (C,D). The model generated values for each subject by adding random variance to their averaged overshoot across all retinal displacements. The generated variance for each retinal displacement was randomly created using the same parameters found in the data. Similar filled symbols denote similar horizontal-vertical components for oblique-fixation pointing directions: 15° left-up (filled squares), 5° left-up (filled circles), 5° right-down (filled crosses), and 15° right-down (filled diamonds). For comparison, a slope of unity (solid line) is included

Table 1 Slopes and correlation coefficients of horizontal and vertical eye drift occurring for gaze direction during (fixation point) F illumination and pointing response

Subject	Horizontal		Vertical	
	r^2	Slope	r^2	Slope
DH	0.004	1.101	0.015	0.187
DL	0.057	-0.289**	0.000	0.002
EK	0.045	-0.376**	0.005	0.121
JC	0.029	1.114*	0.262	0.382**
MC	0.033	-0.715*	0.062	0.275**
MS	0.000	-0.044	0.048	0.328*
Mean	0.084	-0.069	0.065	0.216

*Significant at $P < 0.01$; **significant at $P < 0.001$



one-dimensional analyses by treating horizontal (Fig. 5A,C) and vertical (Fig. 5B,D) error components separately. Thus, if the channel hypothesis of error origin was correct, the data should fall neatly on the slope of unity (solid line in Fig. 5) and a x - y scatter plot should show a high correlation.

Before describing this test, it is necessary to describe two controls. First, a failure to find a correlation in this test could arise from random variations in either the behavior or measurement apparatus, or simply because of the small spread along the abscissa. To control for this, we looked at the consistent predictability of pointing errors within a constant task condition. As mentioned in the Materials and methods section, pointing during cardinal fixation was conducted in consecutive trials with a brief rest in between. Pointing errors from the first set of trials were plotted as function of pointing errors from the second set along both the horizontal and the vertical dimension. This produced mean correlation coefficients (r^2) of 0.97 and 0.80, respectively. This implies that most of the variance had been taken into account and that those errors were consistent across trials in the given data range. This “consistency control” lent validation to our proposed test, but also set upper limits for the expected correlations.

Second, a spurious correlation could arise simply from common trends in the data, e.g., the trend to overshoot. To control for this, we devised a simple quantitative model in which the “subject” overshoot the target by a fixed amount, and a random vertical and horizontal distortion for each side of retinal stimulation. These values (mean overshoot and variance) were derived for individual subjects and used in the model to generate realistic predictions. In this model, any real linearity was removed by the random order process by which variance was added to the mean. Nevertheless, when we applied our test to this generated data, it produced the spurious linear relations shown in Fig. 5A,B. Performing this test ten times for each subject and then comparing across subjects, this generated correlation coefficients of 0.36 ± 0.18 for horizontal and 0.39 ± 0.22 for vertical components. Thus, testing the control data would need to give significantly higher values than these to signify any real linear summation across channels.

Figure 5C,D shows the test for the “best” individual subject, in the sense that this subject showed a typical correlation ($r^2=0.723$) for the horizontal components (Fig. 5C) and the highest individual correlation ($r^2=0.503$) for the vertical components (Fig. 5D). The scatter plots were quasi-linear, although less so in the vertical dimension (Fig. 5D). The individual slopes and correlation coefficients (r^2) for all subjects are shown in Table 2. There was considerable variation between subjects in the power of predictability of this test. Looking across subjects, it does appear that the channel hypothesis predicted most of the variations in the horizontal pointing error (75.0% on average) and over a third of the variations in the vertical pointing error (36.9% on average). The variation predicted by the channel hypothesis

Table 2 Slopes and correlation coefficients of pointing errors during oblique fixation as a function of errors during cardinal fixation

Subject	Horizontal		Vertical	
	r^2	Slope	r^2	Slope
DH	0.724	0.744**	0.503	0.346*
DL	0.812	0.970**	0.135	0.500
EK	0.377	0.621*	0.431	0.246
JC	0.941	0.714**	0.481	0.531
MC	0.900	0.627**	0.250	0.288
MS	0.747	0.904**	0.412	0.315
Mean	0.750	0.768	0.369	0.371

*Significant at $P < 0.01$; **significant at $P < 0.001$

was significantly higher than that predicted by the overshoot model for the horizontal pointing errors (pairwise t -test across subjects, $t(5)=4.22$, $P < 0.01$), but the same was not true for the vertical component ($P > 0.10$). Likewise, the regression slopes for the horizontal data were significantly different from zero for all of the subjects. However, with the exception of one subject, slopes for the vertical data were not significantly different from zero (Table 2).

Thus the two-channel model provided significantly better linear predictability along the horizontal axis than the overshoot model control, but provided about the same degree of linear predictability as the overshoot model control along the vertical axis (Fig. 5A,B). However, the linear summation model still left a considerable amount of the variance in both data sets unaccounted for, compared with our earlier consistency control (e.g., 25.0% for horizontal, 63.1% for vertical). In summary, the linear summation model accounted for most of the variance in the data, but some of this could have been spurious (re the overshoot control), and some of the variance remained completely unaccounted for. The sources of this remaining variance are documented in the remainder of this paper.

Pointing error magnitude as a function of retinal displacement direction

Since pointing errors were only moderately predictable from a linear model, we next quantified the remaining nonlinearities and discontinuities as a function of the direction of retinal displacement. We represented retinocentric target direction with the use of a polar coordinate system (Fig. 6A), running in a counterclockwise direction such that 0° is right and 90° is up, etc. We first plotted the overall *magnitude* of localization errors (relative to controls) against the various directions of retinal displacement. Since we have already shown that retinal displacement magnitude influences pointing error magnitude (Fig. 2) and could confound the direction effect, this variable was held constant at 15° in the current analysis (the symbols joined by the line in Fig. 6A).

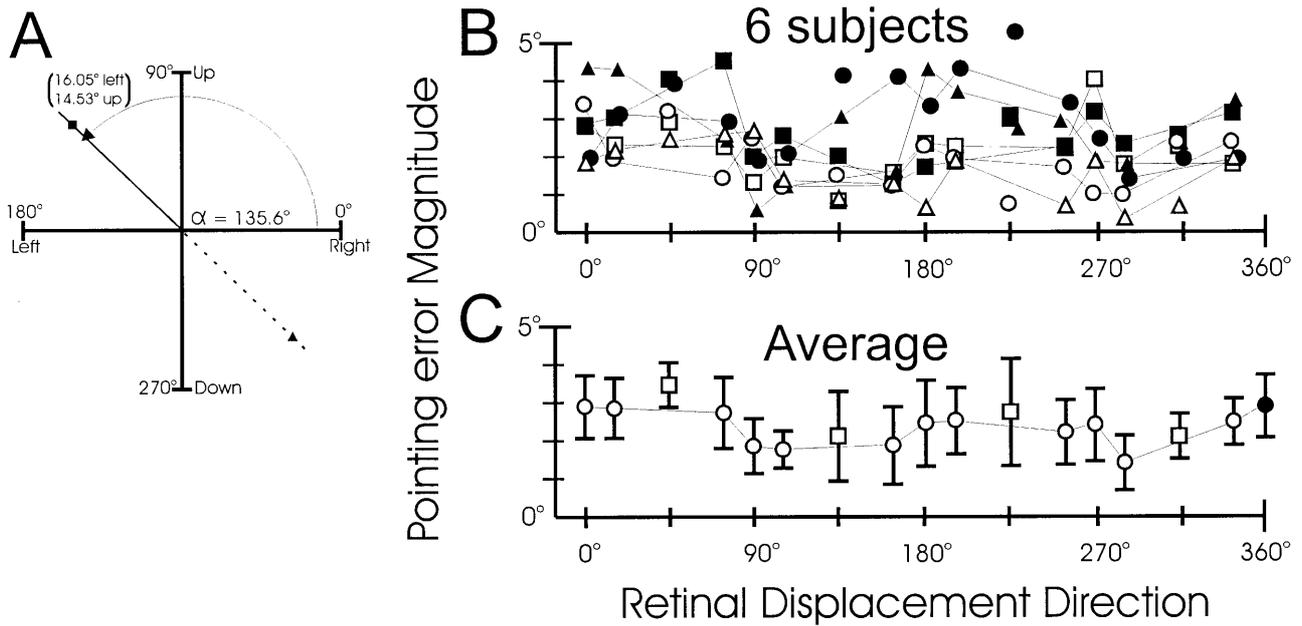


Fig. 6A–C Magnitude of pointing errors as a function of the retinal displacement direction for cardinal and nonstandard oblique retinal displacements (*empty circles*), and for standard oblique retinal displacements (*empty squares*). **A** demonstrates how retinal displacement directions (*filled squares, solid line*) were determined in polar coordinates (α) for mean pointing data, across trials, while fixating the down-right standard oblique LED. Retinal displacement direction was ascertained by simply reversing fixation direction (*filled triangles, dashed line*). **B** Mean results for each subject (*all symbols*). **C** Mean results across subjects. *Symbols joined by a line* denote a similar magnitude of retinal errors ($\approx 15^\circ$); *vertical bars* indicate SEMs across subjects; *filled circle* indicates a repetition of the first data point in **C**

Figure 6B shows the magnitudes of pointing errors averaged across trials for each subject; Fig. 6C shows a further mean across subjects. Across the different retinal displacement directions, the changes in pointing error magnitude were within 40% of the mean, showing a relatively consistent magnitude in the effect. However, there was a tendency (not significant) for pointing error magnitudes to be slightly larger for retinal displacement directions in the up-right (0° – 90°) and down-left (180° – 270°) quadrants than for the other two quadrants, with fairly abrupt transitions between these quadrants. A pairwise *t*-test across subject means showed a significant difference between the third (180° – 270°) and fourth (285° – 360°) quadrants [$t(17) = -2.795$, $P = 0.012$] but not among the other quadrants. A further averaging across all retinal displacement directions (not shown) produced an overall mean magnitude of pointing error of 2.38° ($\pm 0.50^\circ$ SD) for all data points, and a mean of 2.30° ($\pm 0.45^\circ$ SD) for retinal displacement directions with a magnitudes of only $\approx 15^\circ$ (empty circles in Fig. 6B).

Dependence of pointing error direction on retinal displacement direction

The next step in our analysis was to examine the effect of retinal displacement direction on the direction of pointing errors. If indeed the pointing errors were due to misperceptions of retinal displacements, it would make sense to also measure the pointing direction errors in retinal coordinates, as shown in Fig. 7A. Here, error in pointing direction is quantified as the angle between the retinal displacement vector (**RD**) from *F* to the target (*T*), and the “perceived target” vector (**PT**) running from *F* to the actual pointing response (empty circle in Fig. 7A) relative to the controls. The pointing response shown in Fig. 7A (empty circle) is taken from the mean data for one target across subjects in Fig. 7B (empty circle).

Figure 7C–H shows these retinocentric pointing direction errors, averaged across trials, for each subject, plotted against retinal displacement direction in the same polar coordinate system used in Fig. 6A. As is evident from the grand mean of these responses (Fig. 7B), most subjects showed a large clockwise peak in retinocentric pointing direction error for upward retinal displacements (90°), a smaller clockwise peak for downward retinal displacements (270°), and another small counterclockwise peak near the leftward visual field (180°). The transition between the peaks was smooth on average, although individual subjects showed some discontinuities, particularly in the up-left quadrant. In general, the small range in deviation of directional errors indicates that subjects primarily made errors in magnitude rather than direction when considered in a retinal frame.

The preceding analysis assumes that these gaze-dependent pointing errors occur strictly in a retinal frame. However, even if they emerge as a function of retinal displacement, as we have contended, it need not mean

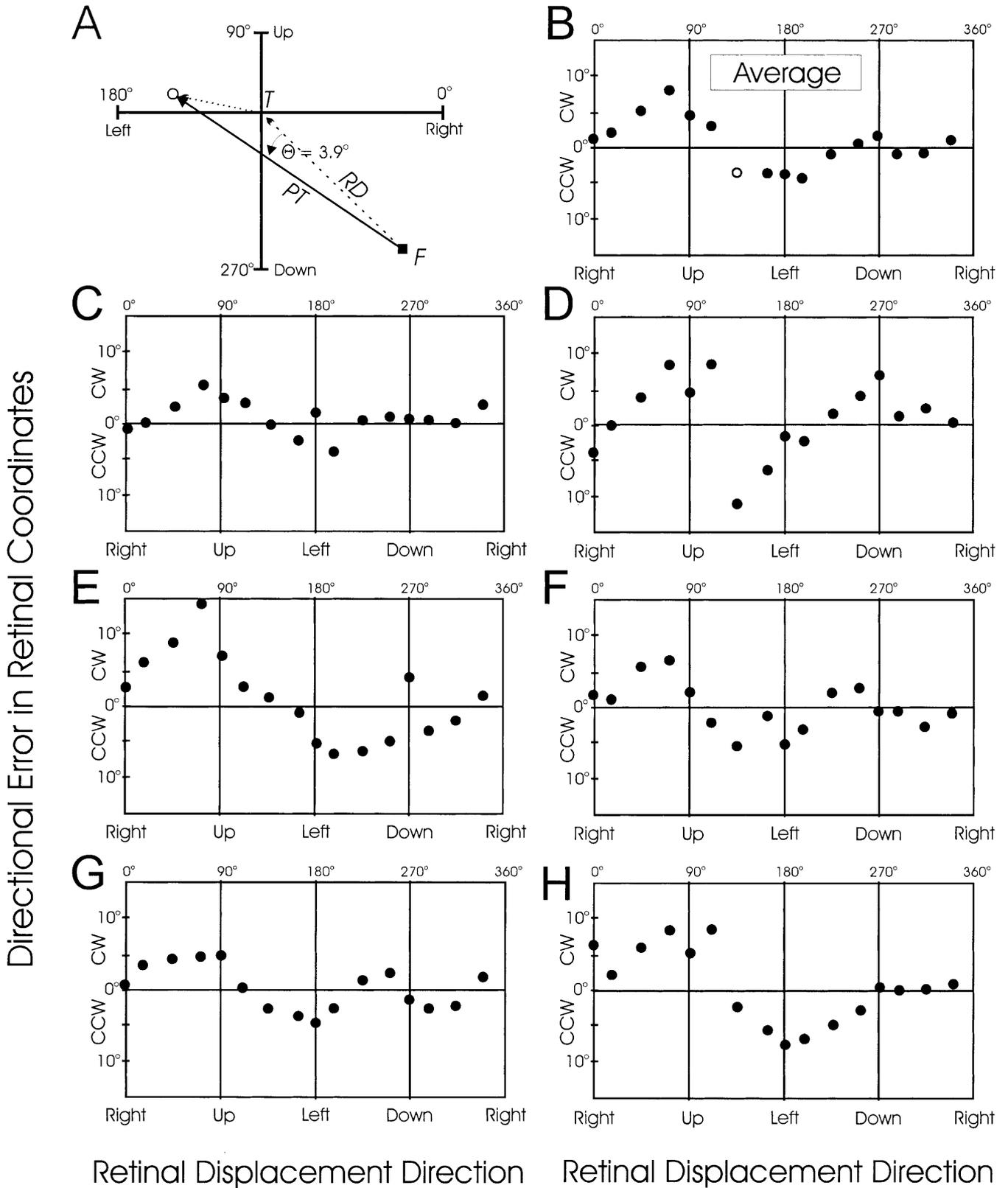


Fig. 7A–H Direction of pointing error in retinal coordinates as a function of direction of retinal displacement. **A** demonstrates how the angle between the retinal displacement vector, **RD** (dashed arrow) and perceived target location vector, **PT** (solid arrow) was

calculated in polar coordinates. Mean results across subjects (**B**) and across trials for each subject (**C–H**). Only pointing results for retinal displacements $\geq 15^\circ$ in length are included

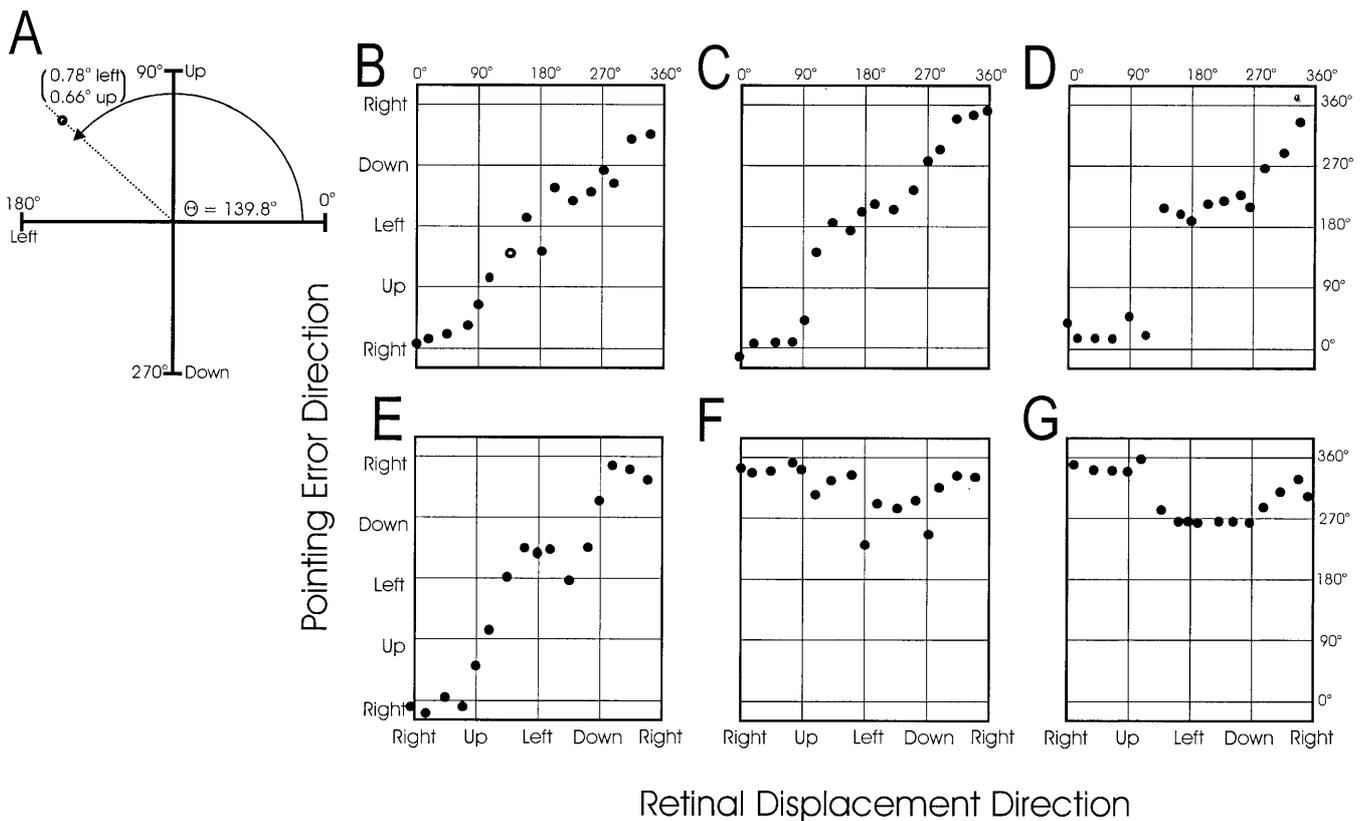


Fig. 8A–G Mean head-centric pointing error direction plotted as a function of mean (across trials) retinal displacement direction, in polar coordinates (**A**) for each subject (**B–G**). Only pointing results for retinal displacements $\geq 15^\circ$ in length are included

that *the output of this function* is also in a retinal frame. For example, even though arm movement-related cells in the posterior parietal cortex seem to be organized in a retinal frame (Snyder et al. 1997; Batista et al. 1999), these cells also have eye position-dependent “gain fields” and are thought to be involved in the initial transformation from retinocentric to head-centric coordinates (Andersen et al. 1985; Batista et al. 1999). Moreover, the geometry of our experiment would produce a large difference between error direction relative to gaze in a retinal frame (Fig. 7A) and error direction relative to controls in a spatial frame. For example, the angular error of spatial mislocation from *T* in Fig. 7A can vary by a much larger angle than that of perceived target (PT) in a retinal frame, because the center of the latter coordinate system is further away. For these reasons, we also quantified the direction of pointing errors in a spatial frame as a function of target direction in a retinal frame.

Figure 8 shows the directions of mean spatial pointing errors plotted against the directions of mean retinal displacements. This time, both pointing errors relative to the control and retinal displacement were quantified in the same polar coordinate system shown in Fig. 6A. For example, Fig. 8A illustrates the direction of mean pointing error for one target in one subject (i.e., from Fig. 8B). In these coordinates, four of the six subjects (Fig.

8B–E) showed a positive slope, indicating localization errors in the direction of retinal displacement. The other two subjects failed to show a positive correlation between retinal error direction and pointing error direction (Fig. 8F–G), showing a more restricted angular range of localization errors. But both patterns showed signs of marked discontinuities at certain points.

To quantify these discontinuities, we plotted the “change” in pointing error (between subsequent points in Fig. 8) in the same polar coordinate system for each subject (Fig. 9A). A linear function would now appear as a flat line, whereas discontinuities would appear as a sharp positive or negative peak. For most subjects, these large changes in pointing errors tended to arise along certain retinal displacement directions. To identify these, we computed 95% confidence intervals for each line. These intervals were computed for each subject across their mean change in pointing errors for each retinal displacement direction. Figure 9B is a frequency histogram showing the number of subjects that exceed each of their confidence interval boundaries for each retinal displacement direction. This individual data formed a roughly bimodal distribution, with most of the significant peaks falling in the upper and lower quadrants.

The systematic locations of these peaks showed up more distinctly when the pointing responses were averaged across all six subjects (Fig. 4) and then similarly converted into change in pointing error as a function of retinal displacement directions in polar coordinates. This line and its 95% confidence interval (as computed for the mean data across subjects for each retinal displacement

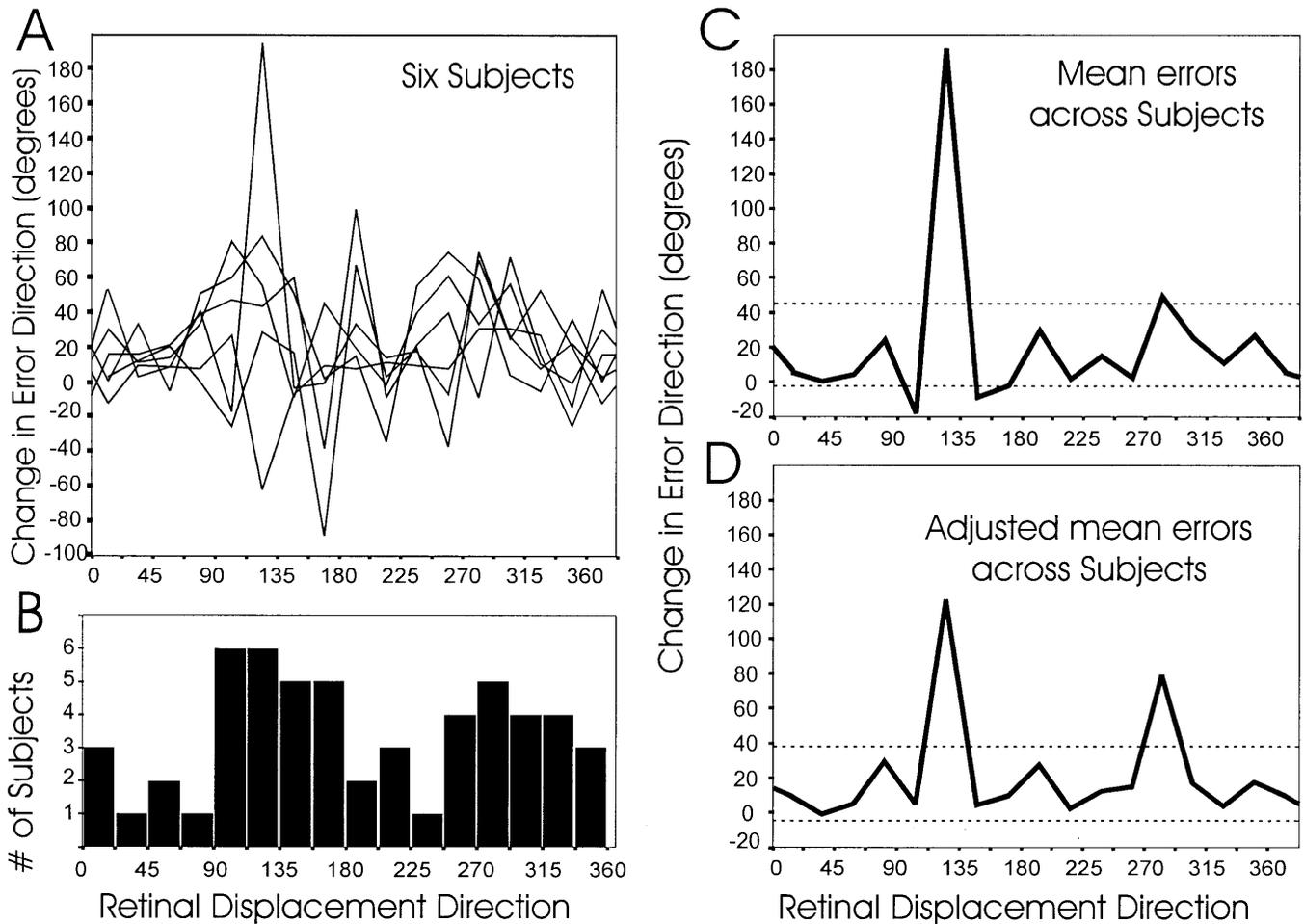


Fig. 9A–D Change in head-centric pointing error direction between adjacent directions of retinal displacement, in polar coordinates. **A** Results for all six subjects and their averaged confidence intervals. **B** Frequency histograms showing the number of subjects in **A** with changes in error direction falling outside the 95% confidence interval for each retinal displacement direction. **C** Similar to **A**, but for the averaged pointing error directions across subjects. Note that this is not the same as averaging the processed data from **A**, which gives a poorer signal-noise ratio in this test. *Dashed line*, 95% confidence intervals. **D** Mean change in pointing error direction across subjects after adjustment for a hypothetical additional downward bias in nonfoveal targets. Downward bias was calculated as the displacement from vertical center when all pointing responses across retinal displacement direction were averaged. The adjustment was made by shifting all the data upward by the same magnitude and subsequently recalculating the adjusted pointing error direction

direction) are plotted in Fig. 9C. This shows four significant peaks (two positive and two negative outside the confidence interval) located close to the vertical meridian ($90^\circ/270^\circ$). The retinal location of the large discontinuity (up-left) corresponds to the uneven distribution of pointing results in Fig. 4, as revealed by the absence of pointing data in the upper-left quadrant (Fig. 4I).

One possibility is that these discontinuities were an artifact of a bias term interacting with our polar coordinate plot. For example, the data for subjects in Fig. 8F,G could act like a bias on the other data. However, remov-

ing these data from the complete data pool did not significantly alter the pattern. Another similar source of bias could have appeared only in nonfoveal targets and were thus not corrected for by subtracting the control response. In particular, averaged, nonfoveal pointing responses showed a bias of 0.79° less than the mean control. To ensure that these discontinuities, in the direction of pointing errors, were not due to this downward pointing bias, we shifted the pointing data upward accordingly and recomputed the adjusted pointing error direction. Adding this constant vertical offset ensures that large changes in pointing error direction were not due to asymmetrical distribution of errors across the horizontal meridian. Figure 9D shows these averaged, adjusted change in error direction (across subjects) plotted against mean retinal displacement direction, and the corresponding 95% confidence interval (dashed line). Although the small negative discontinuities disappeared, the positive discontinuities were upheld and therefore could not have been caused solely by biases in pointing behavior. However, the upward discontinuity (at 125°) was reduced while the downward (at 270°) one increased, making the two discontinuities more similar in size.

Discussion

The current study demonstrates that subjects make small systematic errors in locating remembered targets across various directions of retinal displacement, despite the invariant motor requirements of the tasks. First, although trial-to-trial precision was quite high ($SD < 1^\circ$), subjects consistently pointed below the remembered central target in all experimental conditions, independent of fixation direction. The same vertical bias was also observed in our previous study (Henriques et al. 1998). This bias may be purely motor in origin. For example, pointing bias may reflect a consistent misestimation of desired joint angles or initial hand position that, in turn, could systematically affect final pointing direction (Vindras et al. 1998). This underscores the importance of controlling for the motor aspects of this task, such that motor biases can be reliably subtracted out to isolate the gaze-dependent errors.

Once the bias was corrected for, a systematic distortion of angular retinal displacement was found for retinal displacements in the horizontal, vertical, and oblique directions during open-loop pointing toward the visual targets. When averaged across subjects, the distortion of vertical and oblique retinal displacements was similar to the systematic overestimation of retinal displacement found for horizontal peripheral targets in the current and previous studies (Bock 1986, 1993; Enright 1995; Henriques et al. 1998). However, individual subjects in the current study showed complex variations of this pattern, including variations in the magnitude and direction of retinal distortion across different areas of the visual field.

The direction of pointing errors, in both retinal (Fig. 7) and spatial (Fig. 8) coordinates, was also generally consistent with the direction of retinal displacement. However, there were considerable fluctuations for both measures of error as a function of gaze direction (Fig. 7). For averaged directional errors in retinal coordinates, pointing errors deviated clockwise from retinal displacement direction for upward and downward gaze directions, while deviating more counterclockwise for leftward retinal displacements. However, this pattern of vertical errors tended to vary across subjects, who exhibited different peak-to-peak distances and amplitudes (Fig. 7C–H). Quantifying this retinal-exaggeration effect illustrates the importance of controlling for gaze direction in any study that uses open-loop pointing direction as an indicator of neural function, particularly in light of the intersubject variability of these effects.

As described in the Introduction, these visuomotor miscalibrations may reflect the part of the algorithmic formula employed by the brain in mapping or reading out mnemonic sensory information onto a motor map. If these miscalibrations originated from the visuomotor readout mechanism for separate sites on the retinotopic representation, they could potentially produce completely independent local effects (Miller 1996). Another possibility is that the calibration process is “global” in nature, such that miscalibrations along one area of the vis-

uomotor map generalize to other sections (Vetter et al. 1999), or at least within two independent coordinate channels (Soechting and Flanders 1989a, 1989b). The third possibility is that some compromise exists between the two.

In terms of their gaze-centered frame of reference (Henriques et al. 1998), our results are consistent with those of Vetter and colleagues (1999). However, whereas they found a homogeneous recalibration for a single calibration stimulus, our results comment more on the normal calibration of the system exposed to numerous natural stimuli. Several of these results were consistent with visuomotor calibration studies that suggested a quasi-independent or “semi-local” calibration between the visual and motor systems, upstream from any modular coordinate system (Bedford 1989, 1993, 1994; Ghilardi et al. 1995; Ghahramani et al. 1996). However, even in a quasi-independent system of visuomotor calibration, the spatial calibration function could produce a constant homogeneous effect independent of location in visuomotor space, or it could produce a more “patchy” influence with discontinuities between the patches. Such discontinuities, manifested as sudden deviations in the magnitude or direction of the otherwise systematic exaggeration effect, could adhere to a certain organization, perhaps along known anatomical or physiological discontinuities in the cortical representations of visual space such as the vertical meridian dividing the two hemispheres or the horizontal division between the upper and lower visual fields.

Moreover, the findings in the current study suggest that visuomotor calibrations are not completely independent across vertical and horizontal sites in the retinotopic map, and therefore at best can only be partially attributed to errors within a horizontal-vertical coordinate system. Partial independence of calibration was demonstrated in Fig. 5, where pointing error directions for oblique retinal displacements were only moderately related to the vector sum of pointing errors from the corresponding cardinal retinal displacements. This relationship was particularly weak for the vertical components of oblique pointing responses, with less than half of the variance (36.9%) accounted for by the combined errors of the corresponding cardinal retinal displacements. Overall, the coordinate system hypothesis could explain only about half (56%) of the total variance, and some of this predictive power may have been spurious. However, this does contradict the idea that a coordinate system might be used downstream from the site of these nonsystematic errors, and our data support the idea that *some* of the systematic errors arose within such a coordinate system.

Assuming that much of the visuomotor calibration error arose upstream from any motor coordinate system, the discontinuities observed in our data would seem to indicate that the process was not entirely homogeneous across the visual field. Presumably, these direction-dependent variations could be responsible for some of the unaccounted variance of the linear summation test in Fig. 5. Most of these discontinuities occurred as individ-

ual idiosyncrasies, but some were more consistent, when averaged across subjects, possibly reflecting real physiological discontinuities in retinal representation. For example, small fluctuations in pointing error magnitude as a function of quadrant (Fig. 6C) might correspond to the separate representations of these four quadrants in the striate and extrastriate cortices, with a propensity for upper and lower visual fields to be represented ventrally and dorsally, respectively, across these visual areas (Serenio et al. 1995).

Even more intriguing was the nature of these discontinuities in the range of pointing error directions for retinal displacements in the upward and downward directions in Figs. 8 and 9. In particular, analysis of the change in pointing error direction shows that the discontinuities tended to fall along the vertical axis of the visual field, in all subjects. One possibility is that the discontinuity is due to a shift in ocular dominance with target direction. If subjects, in the attempt to align the target, finger, and dominant eye (McIntyre et al. 1997; Soechting and Flanders 1989a), switch to right-eye dominance abruptly when looking left and vice versa when looking right, then this could be consistent with the observed pattern. However, this seems unlikely to account for the abrupt discontinuities that we observed close to the center of the range.

A second possibility is that the discontinuity may indicate the point of segregation between contralateral representations of visuomotor space in the left and right cortices. While the local calibration of one visual field would be confined to the contralateral side of the brain, the representation of nearly vertical retinal displacements may border on a physiological gap where the spatial representation in one hemisphere ends and the other begins. However, note that the discontinuity across the vertical meridian of the visual field, in Fig. 8, was not perfectly vertical in space but was consistently tilted in the counterclockwise direction with respect to the gravitational vector. Consequently, if our argument that this discontinuity represents the break between the left and right hemisphere representation of visual space holds, then the cortical division in the visual-spatial representation of left and right pointing space may not be as symmetric as one might assume. An interesting question would be whether subjects tested with the opposite eye or arm would show the opposite symmetry.

In conclusion, subjects exhibit a systematic, gaze-dependent distortion of the visuomotor field for pointing. When collapsed across subjects and plotted relative to controls, the nature of the distortion in pointing results yielded a gaze-dependent exaggeration of retinal displacement, with certain discontinuities in direction and magnitude of pointing error as a function of retinal displacement direction. These errors, the probable result of miscalibrations in the visuomotor readout mechanism, were quasi-independent for specific parts of retinotopic maps. Compared with the more global alternatives, this "quasi-local" calibration hypothesis could account for most of our findings and parsimoniously explain the ob-

served variability and discontinuities in visuomotor miscalibrations across the 2-D visual map.

Acknowledgements This work was supported by a Natural Science and Engineering Research Council of Canada Grant to J.D.C and the A. P. Sloan Foundation. J.D.C is a Canadian Medical Research Scholar and was an Alfred P. Sloan Fellow during the course of this study. D.Y.P.H. holds an E. A. Baker Foundation-CNIB/MRC doctoral research award. The authors thank Tutis Vilis, Eliana Klier, Michael Smith, and Melike Ceylan for helpful comments. We also acknowledge the contributions of an anonymous referee in carefully guiding the progress of this paper.

References

- Adamovich SV, Berkinblit MB, Fookson O, Poizner H (1998) Pointing in 3D space in remembered targets. I. Kinesthetic versus visual target presentation. *J Neurophysiol* 79:2833–2846
- Andersen RA, Essick GK, Siegel RM (1985) Encoding of spatial location by posterior parietal neurons. *Science* 230:456–458
- Batista AP, Snyder LH, Andersen RA (1999) Reach plans in eye-centered coordinates. *Science* 285:257–260
- Bedford FL (1989) Constraints on learning new mappings between perceptual dimensions. *J Exp Psychol Hum Percept Perform* 15:232–248
- Bedford FL (1993) Perceptual and cognitive spatial learning. *J Exp Psychol Hum Percept Perform* 17:517–530
- Bedford FL (1994) Of computer mice and men. *Curr Psychol Cogn* 13:405–426
- Bock O (1986) Contribution of retinal versus extraretinal signals towards visual localization in goal-directed movements. *Exp Brain Res* 64:476–482
- Bock O (1993) Localization of objects in the peripheral visual field. *Behav Brain Res* 56:77–84
- Bock O, Eckmiller R (1986) Goal-directed arm movements in absence of visual guidance: evidence for amplitude rather than position control. *Exp Brain Res* 62:451–458
- Bockisch CJ, Miller JM (1999) Difference motor systems use similar damped extraretinal eye position information. *Vision Res* 39:1025–1038
- Caminiti R, Ferraina S, Johnson PB (1996) The sources of visual information to the primate frontal lobe: a novel role for the superior parietal lobule. *Cereb Cortex* 6:319–328
- Caminiti R, Ferraina S, Mayer AB (1998) Visuomotor transformations: early cortical mechanisms of reaching. *Curr Biol* 8:753–761
- Crawford JD (1994) The oculomotor neural integrator uses a behavior-related coordinate system. *J Neurosci* 14:6911–6923
- Crawford JD, Guitton D (1997) Visual-motor transformation required for accurate and kinematically correct saccades. *J Neurophysiol* 78:1447–1467
- Enright JT (1995) The non-visual impact of eye orientation on eye-hand coordination. *Vision Res* 35:1611–1618
- Flanders M, Tillery SIH, Soechting JF (1992) Early stages in a sensorimotor transformation. *Behav Brain Sci* 15:309–362
- Funahashi S, Bruce CJ, Goldman-Rakic PS (1990) Visuospatial coding in primate prefrontal neurons revealed by oculomotor paradigms. *J Neurosci* 63:814–831
- Gauthier GM, Nommay D, Vercher J (1990) The role of ocular muscle proprioception in visual localization of targets. *Science* 249:58–60
- Gentilucci M, Negrotti A (1994) Dissociation between perception and visuomotor transformation during reproduction of remembered distances. *J Neurophysiol* 72:2026–2030
- Ghahramani Z, Wolpert DM (1997) Modular decomposition in visuomotor learning. *Nature* 386:392–395
- Ghahramani Z, Wolpert DM, Jordan MI (1996) Generalization to local remapping of the visuomotor coordinate transformation. *J Neurosci* 16:7085–7096

- Ghilardi MF, Gordon J, Ghez C (1995) Learning a visuomotor transformation in a local area of work space produces directional biases in other areas. *J Neurophysiol* 73:2535–2539
- Goldberg ME, Bruce CJ (1990) Primate frontal eye fields. III. Maintenance of a spatially accurate saccade signal. *J Neurosci* 64:489–508
- Gnadt JW, Bracewell RM, Andersen RA (1991) Sensorimotor transformation during eye movements to remembered visual targets. *Vision Res* 31:693–715
- Henriques DYP, Crawford JD (1998) Visual-motor miscalibrations of remembered vertical and oblique retinal errors when pointing. *Soc Neurosci Abstr* 24:2
- Henriques DYP, Klier EM, Smith MA, Lowy D, Crawford JD (1998) Gaze-centered remapping of remembered visual space in an open-loop pointing task. *J Neurosci* 18:1583–1594
- Hill AL (1972) Direction constancy. *Percept Psychophys* 11:175–178
- Hore J, Watts S, Vilis T (1992) Constraints on arm position when pointing in three dimensions: Donder's law and the Fick gimbal strategy. *J Neurophysiol* 68:1–10
- Imamizu H, Uno Y, Kawato M (1995) Internal representations of the motor apparatus: implications from generalization in visuomotor learning. *J Exp Psychol Hum Percept Perform* 21:1174–1198
- Klier EM, Crawford JD (1998) Human oculomotor system accounts for 3-D eye orientation in the visual-motor transformation for saccades. *J Neurophysiol* 80:2274–2294
- Martin TA, Keating JG, Goodkin HP, Thach WT (1996) Throwing while looking through prisms. II. Specificity and storage of multiple gaze-throw calibrations. *Brain* 119:1199–1211
- Masino T, Knudsen EI (1993) Orienting head movements resulting from electrical microstimulation of the brainstem tegmentum in the barn owl. *J Neurosci* 13:351–370
- McIntyre J, Stratta F, Lacquaniti F (1997) Viewer-centered frame of reference for pointing to memorized targets in three-dimensional space. *J Neurophysiol* 78:1601–1618
- Miller JM (1996) Egocentric localization of a perisaccadic flash by manual pointing. *Vision Res* 36:837–851
- Morgan CL (1978) Constancy of egocentric visual direction. *Percept Psychophys* 23:61–68
- Moschovakis AK, Highstein SM (1994) The anatomy and physiology of primate neurons that control rapid eye movements. *Annu Rev Neurosci* 17:465–488
- Munoz DP, Pelisson D, Guitton D (1991) Movement of neural activity on the superior colliculus motor map during gaze shifts. *Science* 251:1358–1360
- Ogle KN (1964) Research in binocular vision. Hafner, New York
- Schall JD (1995) Neural basis of saccade target selection. *Rev Neurosci* 6:63–85
- Sereno MI, Dale AM, Reppas JB, Kwong KK, Belliveau JW, Brady TJ, Rosen BR, Todoroff RBH (1995) Borders of multiple visual areas revealed by functional magnetic resonance imaging. *Science* 268:889–893
- Soechting JF, Flanders M (1989a) Sensorimotor representations for pointing to targets in three-dimensional space. *J Neurophysiol* 62:582–594
- Soechting JF, Flanders M (1989b) Errors in pointing are due to approximations in sensorimotor transformations. *J Neurophysiol* 62:595–608
- Snyder LH, Batista AP, Andersen RA (1997) Coding of intention in the posterior parietal cortex. *Nature* 386:167–170
- Tweed D, Cadera W, Vilis T (1990) Computing three dimensional eye position quaternions and eye velocity from search coil signals. *Vision Res* 30:97–110
- Vetter P, Goodbody SJ, Wolpert DM (1999) Evidence for an eye-centered spherical representation of the visuomotor map. *J Neurophysiol* 81:935–939
- Vindras P, Desmurget M, Prablanc C, Viviani P (1998) Pointing errors reflect biases in the perception of the initial hand position. *J Neurophysiol* 79:3290–3294
- Waitzman DM, Ma TP, Optican LM, Wurtz RH (1991) Superior colliculus neurons mediate the dynamic characteristics of saccades. *J Neurophysiol* 66:1716–1737