RESEARCH ARTICLE

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Geometric computations underlying eye-hand coordination: orientations of the two eyes and the head

Abstract Eye–hand coordination is geometrically complex. To compute the location of a visual target relative to the hand, the brain must consider every anatomical link in the chain from retinas to fingertips. Here we focus on the first three links, studying how the brain handles information about the angles of the two eyes and the head. It is known that people, even in darkness, reach more accurately when the eye looks toward the target, rather than right or left of it. We show that reaching is also impaired when the binocular fixation point is displaced from the target in depth: reaching becomes not just sloppy, but systematically inaccurate. Surprisingly, though, in normal Gaze-On-Target reaching we found no strong correlations between errors in aiming the eyes and hand onto the target site. We also asked people to reach when the head was not facing the target. When the eyes were on-target, people reached accurately, but when gaze was off-target, performance degraded. Taking all these findings together, we suggest that the brain's computational networks have learned the complex geometry of reaching for well-practiced tasks, but that the networks are poorly calibrated for less common tasks such as Gaze-Off-Target reaching.

Introduction

Eye–hand coordination has played a major role in human culture and evolution, but we are just beginning to appreciate its complexity. To reach for an object, the brain identifies the object's images in both retinas and finds its directions relative to the two foveae. To compute the object's location relative to the reaching arm, the brain must consider both eyes' orientations in the head, and the position of the head itself, whose rotation changes the distance between the eyes and the shoulder (Fig. 1). The present study quantifies all the elements in this linkage, binocular eye orientations, eyeball locations,

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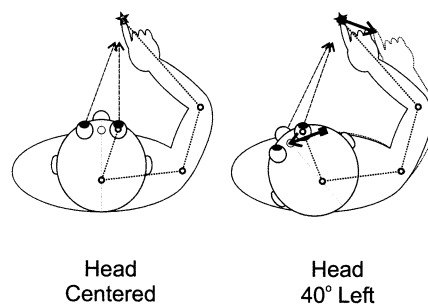York University,
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Head   Head
Centered   40° Left

Fig. 1 Geometry of reaching. *Left* Head is centered, facing the target. *Right* Head is rotated 40° left. Gaze directions are indicated by *dashed lines*. To compute target's location relative to the shoulder, one must use the target image location on the retina, the angle of eye rotation, and the angle of head rotation. Because the rotary centers (*circles*) of the eyes, head, and arm do not coincide, head rotation translates the eyes (*left-pointing arrow*) with respect to the shoulder. If this translation were ignored (Henriques and Crawford 2002), subjects would miscalculate target location in the opposite direction (*right-pointing arrow*)

head orientation, skull, neck and clavicle geometry, and the angles and lengths of the arm segments, to investigate the geometric computations underlying reaching, and in particular the brain's handling of information about the two eyes and the head.

It is known that people reach more accurately when the eyes look straight at the target, rather than right or left of it (Prablanc et al. 1979; Bock 1986; Neggers and Bekkering 1999; Van Donkelaar and Staub 2000; Johansson et al. 2001). This happens even in darkness when the target and hand are no longer visible (Vercher et al. 1994; Henriques et al. 1998; Henriques and Crawford 2000). Here we show that reaching is also impaired when the binocular fixation point, the locus in space where the gaze lines of the two eyes intersect, is displaced from the target in depth; that is, when one eye foveates the target but the other does not. Of course if even one eye fails to foveate the target, then the brain receives less foveal input about its location; some data arrive from the peripheral retina, where visual resolution is lower, so one would expect less precise reaching. Crucially, though, we demonstrate that reaching does not simply become sloppy, as one would expect given the loss of resolution. Rather, people systematically misreach, and this requires another explanation. We investigate this mechanism by looking for correlations between arm control and the binocular fixation point.

To study the brain's handling of head rotation, we asked people to reach when the head, or the head and eyes, were not aimed at the target. Under these conditions, the brain must compute the complex, non-linear influence of head rotation on visual localization. It is known that people are poorer at locating targets when their head rotates away from the body's midline (Biguer et al. 1984; Rossetti et al. 1994; Vercher et al. 1994; McIntyre et al. 1997). Here we explore the geometric computations involved, and test whether the computation changes when the eyes point away from the target.

Materials and methods

Subjects

Subjects were nine right-handers (aged 21–37 years, five male) with no history of sensory, perceptual, or motor disorders. All gave informed consent. One subject was left-eye dominant while the rest were right-eye dominant by the ring test (Crider 1944). The experiments were approved by the ethics committee of the University Medical Center.

Experimental setup

In all our experiments, subjects saw a briefly lit target in the dark and then placed their finger at its remembered site. Subjects sat in a dark room with their torso immobilized by a harness. We measured the three-dimensional (3-D) location and orientation of the head (Medendorp et al. 2000), and the 3-D locations of the eyeballs, shoulder, elbow, index fingertip, and target, all with an Optotrak 3020 system, which works by tracking infrared emitting diodes (IREDs) attached to the targets and the subject's body. Before the

experiments, an additional IRED was temporarily placed on each eyelid. These were recorded along with the IREDs on the helmet to compute the locations of the eyeballs in the head. Using these data, we could reconstruct the eye's locations in space throughout the later experiments from the helmet IREDs alone. Optotrak data were collected at 100 Hz. Two-dimensional *orientations* of the eyes in space were measured using search coils (Collewijn et al. 1975) in three perpendicular magnetic fields generated by Helmholtz coils 3.3 m across (Medendorp et al. 2000). Coil signals were low-pass filtered at 75 Hz (FIR filter; Matlab). Eye-coil data were recorded at 500 Hz.

We analyzed only horizontal motion: horizontal eye and head rotations, and finger and target locations in the transverse plane. Locations were expressed in Cartesian coordinates, *forward* and *sideways*, though some analyses also examined *(cyclopean) depth*, meaning the distance to the target or fixation point from a spot midway between the eyes.

Stimuli

Red light-emitting diodes (LEDs) indicated to the subject where to orient their head. These *head-orienting LEDs* were mounted on a matte black screen 2 m in front of the subject. Seven such LEDs were placed at 10° intervals from 30° left to 30° right, with the central one located in front of one of the subject's eyes. To help guide the head toward the LED, the subject wore a highly attenuated, head-mounted laser that continuously projected a faint dot on the screen (this dot likely had no effect on reaching, as it did not influence pointing in Henriques and Crawford 2002).

Reaching targets were three green LEDs mounted on a movable rod. At the start of each trial, the rod lay in a parasagittal plane, pointing directly at one of the subject's eyes, so that the three LEDs lay one behind the other, 30, 38, and 50 cm from the eye. These LEDs, called the *near*, *middle*, and *far* targets, were vertically staggered by 4 mm so that the nearer lights would not occlude the farther ones. In each trial, one of these LEDs was briefly lit. The subject then reached for it in darkness. At the same time, a computer-driven motor swung the rod away so that the subject's hand would not collide with any of the targets or receive any tactile feedback. Subjects knew that the targets would swing away, so they expected no contact.

Two additional reaching targets lay 5 cm left and right of the near target. These flashed only rarely, to ensure that subjects had to adjust their reaching direction to match the visual target and did not simply make repeated stereotypic responses in the parasagittal plane of the rod. Data for these *catch* targets were excluded from further analysis.

Tasks

There were two tasks, depicted in Fig. 2. The *Gaze-On-Target* task began with one of the seven head-orienting LEDs lighting up for 1.2 s to guide the subject's head to the required posture. Then one of the five reaching targets was randomly selected and lit for 1.3 s while the subject redirected their eyes to fixate it. The target was extinguished, and the subject immediately reached to its remembered location with the right hand. They had 2.3 s to place their finger on the target site and hold it there before an auditory cue told them to return their arm to its resting position beside their hip and prepare for the next trial, which started 1 s later.

The *Gaze-Off-Target* task was identical except that the subject did not move their gaze to the target, which was lit for 1.0 s. Instead, they fixated the head-orienting LED throughout the trial, and saw the target on the peripheral retina.

The central head-orienting LED, at 0°, lay in the same parasagittal plane as the three main reaching targets, so in the case where the head was oriented toward 0°, the only difference between the Gaze-On- and Gaze-Off-Target tasks was the depth of the fixation point: in the Gaze-Off-Target task, subjects fixated 2 m
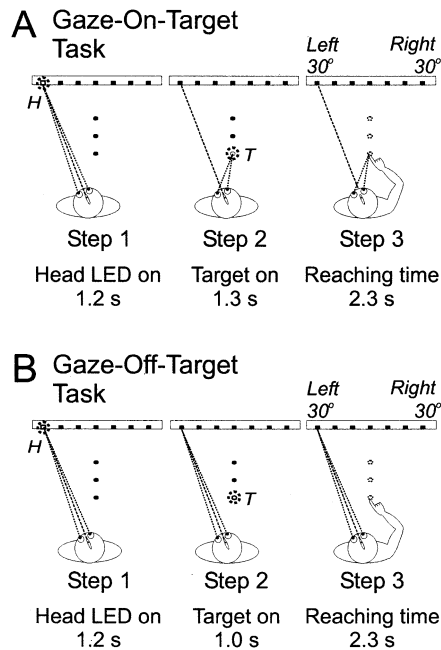
Fig. 2A, B The two experimental tasks, seen from above. *Solid squares* are the seven head-orienting light-emitting diodes (LEDs; *H*); *solid circles* are the reaching targets (*T*). *Open symbols* are lit LEDs. *Dotted circles* mark the former locations of extinguished and removed targets. *Dotted lines* show gaze direction; *dashed lines* show head direction. **A** Gaze-On-Target task. In step 1, subjects rotated their head toward the head-orienting LED, where they held it throughout the trial. In step 2, subjects moved their eyes to the target (visible for 1.3 s), where they maintained fixation even after the target was extinguished and removed in step 3. Subjects then placed their finger on the remembered target location. **B** Gaze-Off-Target task. The task is identical except that subjects kept both head and eyes aimed at the head-orienting LED throughout the trial, never looking to the target (which was visible for 1.0 s). In both tasks, subjects had 2.3 s to place and hold their fingertip on the target site

away, well behind the reaching target. We used this condition to explore the influence of fixation depth on reaching accuracy.

In both tasks the head positioning was time-consuming and confusing for the subject. To speed up the experiment and improve performance, we divided each task into seven sets, one for each head-orienting LED, and presented the sets in a fixed order beginning with the 30° leftward LED and ending with the 30° rightward one. Thus the order of sets was not randomized, but it was the same in both tasks, so performance on the two tasks could be meaningfully compared. Within each set, the main three reaching targets were randomly presented five or eight times each and the catch targets twice each, for a total of 19 or 28 trials. Subjects performed the Gaze-Off-Target task first, so that they could not use their experience with the target array on the easier Gaze-On-Target task to alter their performance.

We addressed three questions:

1. How is reaching influenced by depth of gaze: do people reach inaccurately when they look toward the target but fixate well beyond it? We approached this question by comparing reaching accuracy in the two tasks when the head was facing forward.
2. How do fixation and finger errors correlate in normal reaching? That is, even in Gaze-On-Target tasks, people make small errors in placing their binocular fixation point; do these errors lead to correlated errors in finger placement?

3. How well does the brain handle changes in linkage geometry: do people misreach when the head, or the eyes and head, are directed away from the target, altering the geometric relation between retinal images and the arm? And can their errors be explained by any specific, identifiable miscalculation of head position or body geometry?

Results

Does fixation distance influence reaching?

It is known that the direction of the line of sight influences reaching (Bock 1986, Enright 1995; Henriques et al. 1998; Henriques and Crawford 2002; Medendorp and Crawford 2002; Pouget et al. 2002), but does the distance to the binocular fixation point also play a role? We compared reaching accuracy in five subjects. The subject's head faced straight forward, and the head-orienting LED and the three reaching targets lay in front of the non-dominant eye. In the Gaze-On-Target task (Fig. 3A), both eyes looked at the reaching target. In the Gaze-Off-Target task (Fig. 3B), the eyes looked at the head-orienting LED 2 m away. So in both tasks the non-dominant eye always looked straight ahead, along the line of reaching targets, but in the Gaze-Off-Target case the fixation point lay 2 m away, well beyond the targets.

In this part of the study we measured the orientation of just the dominant eye, but those data confirmed that the subjects looked where they were instructed. In the Gaze-On-Target task, subjects turned the dominant eye, on average, 9.4° medially for the near target, 7.1° for the middle target, and 5.0° for the far target; these are close to the angles needed for perfect binocular fixation of the targets: 10.5°, 7.7°, and 5.3°. In the Gaze-Off-Target task, subjects directed the dominant eye 0.9° medially, where perfect fixation would call for 0.8°. As instructed, then, subjects fixated near the target in one task and far behind it in the other.

Reaching accuracy is shown in Fig. 3, where ellipses mark 95% confidence intervals for final fingertip position (these three ellipses are ordered as one might expect, the bottom one marks the finger positions after reaches to the near target and the top one is for reaches to the far target. The middle row of the figure shows the ellipses for one subject, while the bottom row shows ellipses averaged across all five subjects.

Fixation distance did clearly influence reaching. By a pairwise t-test, reaching errors along the depth dimension were smaller [$t(14)=2.28$, $P<0.02$] in the Gaze-On-Target task than in the Gaze-Off-Target task. In the Gaze-On-Target trials (Fig. 3 *left column*), ellipses for near- and middle-target reaching were centered close to their targets, overshooting the near one by only 2.4 (±8.8, SD) cm and undershooting the middle and far ones by 0.2 (±6.9) and 5.7 (±5.6) cm. In the Gaze-Off-Target trials (Fig. 3 *right column*), the ellipses did not vary consistently with target distance [one-way ANOVA, $F(2,12)=2.11$, $P=0.164$], but instead appeared to be centered near a common 'default' point, overshooting
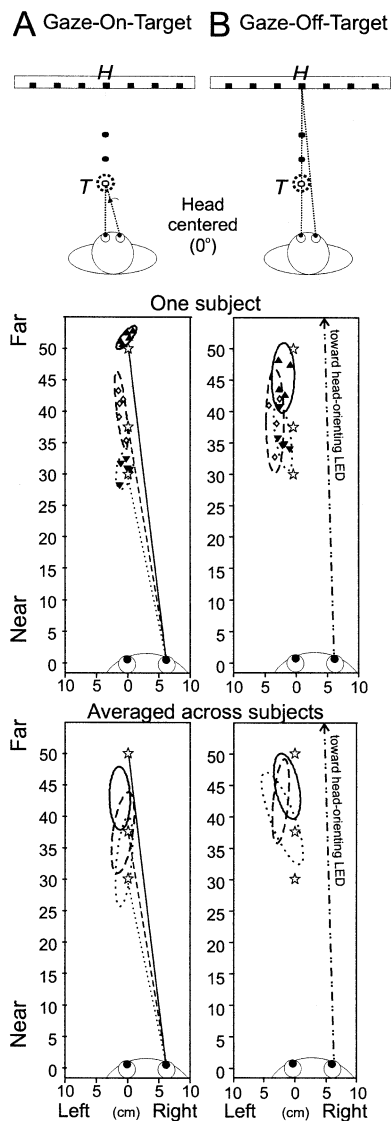
Fig. 3A, B Effect of fixation depth on reaching. **A** Gaze-On-Target task. Both eyes are aimed at the target site, so fixation depth matches target depth. **B** Gaze-Off-Target task. One eye is diverged so that fixation depth is far behind the targets (toward the head-orienting LED). *Middle row* Fingertip locations and their elliptical fits for each target for one subject (these 95% confidence ellipses were computed from the covariance matrices of fingertip locations for each of the three targets in each task). *Inverted triangles* mark reaches to the near target, *diamonds* the middle target, and *upright triangles* the far target. *Stars* mark the target sites. *Bottom row* Averaged ellipses, calculated by averaging across the ellipses for each of the five subjects: *solid-line ellipses* for far targets, *dashed* for middle targets, and *dotted* for near targets

the near and middle targets by 9.9 (±5.2) and 4.7 (±3.6) cm, and undershooting the far one by 4.9 (±5.2) cm. In the Gaze-On-Target task, reaching shifted more with target distance, as shown by the near-significant correlation [$F(2,12)=3.723$, $P=0.055$]. That is, placing the gaze point at the correct depth did improve reaching in the forward dimension.

The crucial point is that failure to foveate the target with both eyes caused not merely variable reaching, which could be explained by the lower resolution of the retina away from the fovea, but also consistent errors. We shall consider the mechanism in the Discussion, taking into account data from the following two sections on binocular fixation.

How accurate is binocular fixation?

Previous studies of gaze-guided reaching have not actually measured the location of the binocular fixation point. In four subjects performing the Gaze-On-Target task we measured the orientations and locations of both eyes, and from those data we computed the locus of binocular fixation, and the ideal angles of the two eyes that would allow perfect fixation of the target. Subjects' actual eye angles (at the end of the reaching movement, long after the target light went off) matched the ideal values reasonably well, with a mean slope of 0.74 (±0.20, SD across subjects for both eyes) and a mean r^2 values of 0.84 (±0.15). We found a similar relation between measured and ideal vergence angles, with a mean slope of 0.89 (±0.10) and a mean r^2 of 0.78 (±0.13). So subjects fairly accurately converged their eyes on the target, though the subunity slopes show that they failed to converge enough, i.e., they fixated beyond the target. On average, their convergence errors amounted to 2.3°, and their binocular fixation point missed the target by about 75 mm. We know these are genuine errors of convergence and not measurement errors on our part, because when we asked subjects to fixate *visible* target lights, the measured convergence angles were near-ideal, with an average vergence error of just 0.4°.

Do eye and hand accuracy correlate in normal, Gaze-On-Target reaching?

In the Gaze-On-Target task, subjects not only failed to fixate the target perfectly, they also varied somewhat trial to trial, usually looking beyond the target but occasionally falling short, sometimes looking right of the target, sometimes left. Are these fixation errors related to errors in reaching?

We fitted ellipses (with 95% confidence intervals) to the cloud of binocular fixation points of each subject for each target. Ellipses for each subject (*thin traces*) are plotted in Fig. 4 along with similar elliptical fits to finger position (*thick traces*) for the three targets (*stars*). In most plots, gaze and fingertip tend to overshoot, especially the two nearer targets, and are biased to the left. But for any one target, the fixation and finger ellipses overlap only partially, and they differ markedly in location, orientation, and shape.

As these plots suggest, reaching errors did not correlate with fixation errors: the mean r^2 was just 0.08 for the sideways components of these errors, 0.02 for their

Fig. 4 Elliptical fits to binocular gaze points and to fingertip location for the three targets for four subjects. *Thin-lined ellipses* are fitted to binocular gaze points; *thick-lined ellipses* to the fingertip locations. For both gaze and finger ellipses, line styles indicate targets: *dotted* for the near target, *dashed* for middle, *solid* for far. Ellipses, symbols, and axes as in Fig. 3
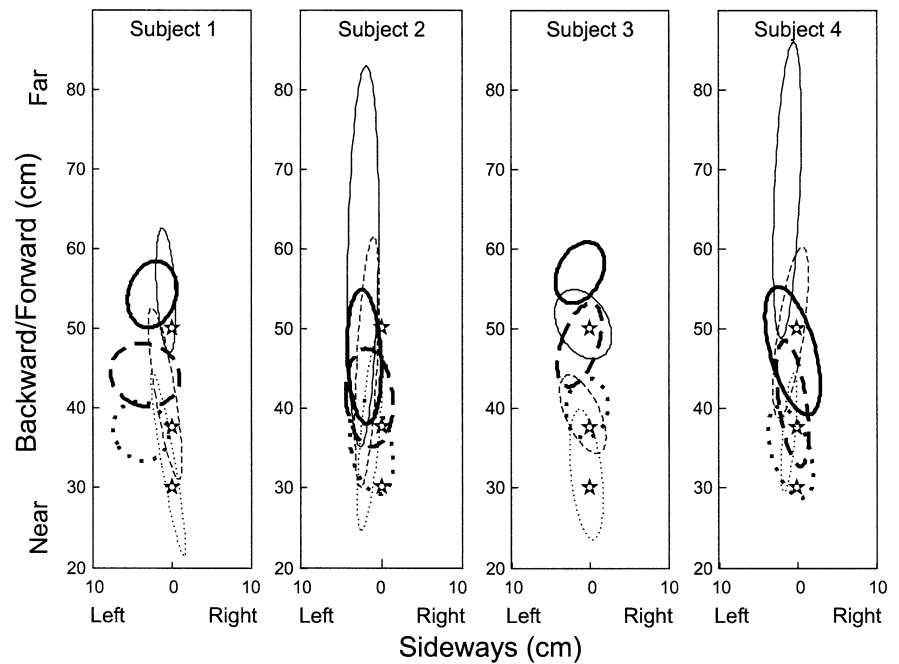
forward/backward components, and 0.01 for their overall magnitudes. We also considered the radial distance, or *depth*, of the target, fingertip and fixation point from the cyclopean eye (midway between the two real eyes). In this sense, the depth components of reaching and fixation errors also failed to correlate: the mean r^2 was just 0.09. In short, subjects did not misreach in the direction of the fixation point, nor did larger deviations in fixation lead to larger mistakes in reaching.

How well does the brain correct for head rotation?

We asked subjects to reach for the same straight-ahead targets while holding their heads in different positions, from 30° left to 30° right. The head rotation between these outermost positions transports the eyes 8 cm sideways, so if the visuomotor system failed to take into account that eye translation, subjects would, for instance, reach 4 cm right of the target when the head was turned 30° left (Fig. 1).

Figure 5 shows an above view of final finger positions averaged across subjects. For each of the three targets, a line connects up the seven symbols representing reaching responses from each of the seven head positions. In the Gaze-On-Target task (Fig. 5A), subjects made some errors: they reached slightly left of the targets, and they overreached the near and middle targets while underreaching the far one, consistent with the 'contraction' or 'range' effect found by others (Soechting and Flanders 1989; Gentilucci and Negrotti 1994; Tresilian et al. 1999). But on the whole their performance was quite accurate. And the different head positions caused no major problems: each constellation of seven symbols is quite compact.
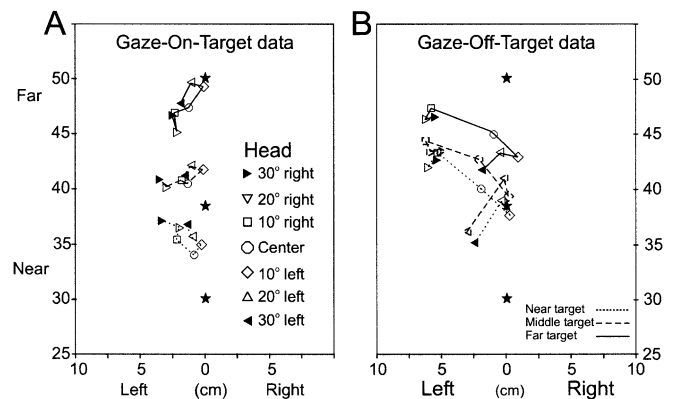

Fig. 5A, B Averaged final fingertip locations for each target and head direction for the Gaze-On-Target task (**A**) and Gaze-Off-Target task (**B**). Results averaged across trials and subjects. Sideways direction is shown along the abscissa and depth along the ordinate starting with the location of the eyes (not shown). Responses for the seven head postures are represented by different symbols (see *key* in **A**). *Dotted lines* join the responses for near targets, *dashed lines* the middle target, and *solids lines* the far target. *Stars* mark the target sites

In the Gaze-Off-Target task (Fig. 5B) the errors were larger, and the responses from different head positions more spread out, i.e., the brain now coped poorly with the effects of head rotation. Displacing both the eyes and the head from the target overtaxed the geometric capabilities of the system.

Are these errors due to miscalculated eye translation?

What exactly goes wrong in the brain's computation? We cannot say for sure, in part because we do not know how
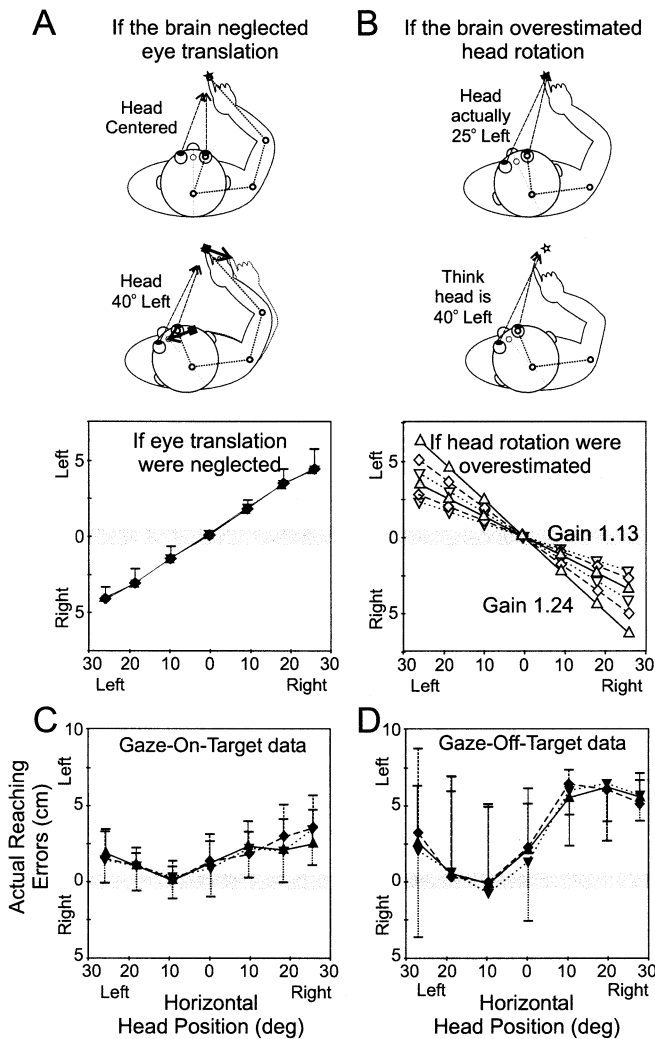
Fig. 6A–D Sideways reaching errors as a function of head position. Symbols as in Fig. 3. **A** Errors subjects would make if they neglected the translation of the (cyclopean) eye caused by head rotation. **B** Errors subjects would make if an overestimate of head rotation influenced their calculation of target location. *White and gray symbols* show the errors predicted if subjects overestimated head rotation by 13% and 24% (the percentages suggested by head-positioning errors in our data and in those of Becker and Saglam 2001). **C** Actual mean errors (averaged across trials and subjects) in the Gaze-On-Target task mimic the upward-sloping pattern in **A**, but only faintly. **D** Actual mean errors in the Gaze-Off-Target task show the same pattern, slightly more strongly. The data in **C** and **D** do not resemble errors predicted in **B**. *Gray shaded bars* indicate the area within 0.5 cm of the actual target site at 0°. *Error bars* represent mean standard deviations across subjects

the computation is organized in the brain; it may use some 'distributed' processing quite different from the equations a mathematician would write down. But part of the error may be attributable to the most intuitively obvious source: a miscalculation of the eye's translation. Figure 6A shows the sideways reaching errors the system *would* make if it completely neglected this translation: when the head is 30° left, the finger reaches 4 cm too far right, when the head is 30° right, the finger reaches 4 cm too far left.

Actual sideways errors in the Gaze-On-Target task (Fig. 6C) show this same pattern, significantly (two-way ANOVA, $F_{(6,167)}=8.8$, $P<0.001$] though only faintly.

Errors in the Gaze-Off-Target task (Fig. 6D) show the same pattern as those in the Gaze-On-Target task, but more strongly [two-way ANOVA, $F_{(6,84)}=6.3$, $P<0.001$]: as the eyes and head turned from left to right, the reaching errors shifted from right to left, though the errors saturated and even declined with head positions beyond 10–20°.

If the reaching errors were entirely explicable as a miscalculation of eye translation, then a plot of actual errors versus the errors predicted in Fig. 6A would yield a straight line of slope 1. If reaching errors were unrelated to eye translation, the slope would be zero. The fitted slopes (not shown) lay between these extremes: for the Gaze-On-Target task, the slope was 0.22 and r^2 was 0.49, and for the Gaze-Off-Target task, the slope was 0.61 and r^2 was 0.57. So part of the error, in the sideways dimension, is consistent with an underestimate of the eyes' translations, in particular for the Gaze-On-Target task. Our subjects' errors in the forward/backward dimension cannot be so explained, because an underestimate of eye translation would cause almost no errors in that dimension.

Another possibility is that these patterns of reaching reflect a misestimate not of eye translation but of the angle of head rotation. Becker and Saglam (2001) found that when subjects were asked to turn the head on the torso, away from straight ahead, to aim their nose at a target, they tended not to turn far enough; for example when required to turn the head 40° they in fact turned it only about 32° (40 is 24% larger than 32.26). Apparently they overestimated how far they were turning their heads by about 24%. In our study, subjects rotated the head only 88% of the indicated amplitude, suggesting that they overestimated their head turns by about 13%. Therefore we considered whether our subjects' reaching errors might reflect an overestimate of head rotation. But that theory, simulated in Fig. 6B, does not fit the data even qualitatively. Nor were we able, by assuming misestimates of both eye translation *and* head rotation, to explain the data any better than we could with the purely translational hypothesis in Fig. 6A. So we found no evidence that an overestimate of head rotation influenced our subjects' reaching.

In summary, our subjects reached fairly accurately from a range of head positions, showing that they were able to compute target location from a mix of signals coding retinal target location, eye translation, and head position. But their performance declined sharply when they looked away from the target.

Discussion

The geometric computations necessary for reaching become more complex when the eyes or the head are allowed to face away from the target. We found that

people misreach when they are asked to hold the binocular fixation point far from the remembered target, in either the sideways or forward-backward dimension; their reaching becomes not just sloppy, but systematically inaccurate. In normal reaching, though, we found no correlation between people's natural, small errors in fixation and their errors in reaching. When asked to reach with the head facing away from the target, people can still aim accurately, but only when they look toward its remembered location.

Fixation during reaching

When subjects were asked to fixate while reaching, their foveae missed the target by about 1.2° on average (half the vergence error of 2.3°), an error about six times larger than that seen when they were asked merely to fixate visible lights in the same locations. But even 1.2° is a small error, given that the fovea is about 5° across (and even the rod-free fovea is 1.7° wide). Perhaps more precise fixation is unnecessary for accurate reaching, so subjects instead adopt more comfortable, less eccentric eye positions. In keeping with this idea, our subjects fixated less accurately when they held their heads more eccentrically. Likewise, for these head postures, the farther of the two eyes sometimes diverged more and as a result shifted the gaze point farther in depth (Brenner and Smeets 2000). Presumably these small inaccuracies do not seriously impair reaching.

Is the fixation point a magnet for the hand?

When we look away from the target our reaching degrades. Why? When we look away, we lose foveal vision of the target and therefore localize it less precisely, but that is not the whole story. Vercher and colleagues (1994) found that people reach more accurately when they look to the target, even if they never foveate it, because it vanishes before they look at it. And in our study, reaching showed not just greater variability, which could have been explained based on the reduced visual acuity away from the fovea, but also consistent, systematic inaccuracy. What is the mechanism for this systematic error?

Some authors have suggested that the gaze point in some sense guides or 'magnetically attracts' the hand (Abrams et al. 1990; Neggers and Bekkering 2000; Soechting et al. 2000). Even in darkness, people can point fairly accurately in their current or recent direction of gaze (Bock 1986; Blouin et al. 1995, 2002), so we know that eye-position information can be used to guide the hand. But of course the issue here is not whether such information helps guide reaching; clearly it must, because without it we could hardly localize visual objects at all. The issue is whether eye-position signals carry inordinate weight, or more precisely, whether the visuomotor system tends to interpret eye-position signals as target-position signals, in effect assuming that the eyes are on-target,

even when the visual data do not support that assumption (Abrams et al. 1990).

Several studies have shown that eye and hand kinematics are correlated in various visuomotor tasks (Prablanc et al. 1979; Fisk and Goodale 1985; Abrams et al. 1990; Vercher et al. 1994; Binsted and Elliott 1999; Kroller et al. 1999; Neggers and Bekkering 1999, 2000; Engel et al. 2000; Sailer et al. 2000; Soechting et al. 2000; Johansson et al. 2001; Pelz et al. 2001), but that is to be expected, given that both are ultimately driven by the same retinal images and that we tend to look at things we reach for simply to see them better, so these findings do not address the 'magnet' issue.

Some patients show 'magnetic' reaching (Carey 2000), but they have cortical damage, possibly to a retinotopic motor map, as in the parietal reach region. As large portions of such maps are devoted to the fovea, a partial lesion might spare some of the foveal representation. Residual activity there might drive the hand abnormally to the foveated point in space. In any case, this finding does not demonstrate a magnetic effect in normal reaching.

If the gaze point attracts the hand, we would expect errors in reaching to correlate with errors in fixation, but no such correlations were seen in our data. Similarly, Prablanc et al. (1979) found no correlation between gaze and pointing errors in a task where subjects looked to a horizontal target after it was extinguished. It is still possible that the gaze point attracts the hand but its effects are obscured—McIntyre et al. (2000) have shown with simulations how later stages of visuomotor processing can mask earlier ones—but at present there seems to be no clear evidence for a magnetic effect in normal, Gaze-On-Target reaching.

Contraction of depth estimates

When subjects reached to remembered targets, they overshot the near ones and undershot the far one (Fig. 3). This is the 'contraction' or 'central tendency' found in many other studies where subjects estimate depth verbally or by pointing, reaching with a stick, or moving a marker (see, for example, Foley 1980, 1985; Soechting and Flanders 1989; Gentilucci and Negrotti 1994; McIntyre et al. 1997; Tresilian et al. 1999). The reaching errors depend on the location of the targets and not on movement amplitude, suggesting that the contraction cannot be explained by mistakes in computing arm displacement (Soechting and Flanders 1989). And the pattern of contraction apparently depends on all the relevant targets: subjects will overestimate the depth of an object 40 cm away when it is the nearest of a set of targets, but underestimate it if it is the farthest (Gogel 1972). To explain this effect, Gogel (1972) proposed that people base their reaching in part on an estimate of 'specific distance', perhaps near the center of the target set, and give that estimate more weight as binocular cues to distance become inadequate. Gogel's mechanism could

therefore explain why our subjects showed more contraction during Gaze-Off-Target reaching, when their retinal signals were less precise (Figs. 2, 3B, 6).

Linkage geometry in the brain

We have shown that the brain takes into account head position and the resulting eye translation when it localizes visible objects, but the localization is imperfect. We tested whether our subjects' errors could be attributed to miscalculations of the two intuitively obvious variables, head rotation and eye translation. The rotation theory was inaccurate, while the translation theory explained qualitative trends in the data but not quantitative details. A more quantitative explanation may have to await more detailed knowledge of the variables and coordinate systems used by the visual localization algorithms in the brain, for example, the errors may arise because the relevant geometric equations are linearized or otherwise simplified, but the consequences of such simplifications depend strongly on the coordinate system in use (Flanders et al. 1992; McIntyre et al. 1998, 2000) and in the case of visual localization, the neural coordinates remain unclear. McIntyre and colleagues (1997, 1998) and Carrozzo et al. (1999) have tried to deduce these coordinates based on reaching errors, but so far the data are ambiguous, at least for reaches in darkness: as these authors have shown, errors arising in the various stages of visuomotor processing can interact and mask one another, obscuring the coordinates (MacIntyre et al. 2000).

We considered visual localization of objects relative to the torso, but other studies have shown that linkage geometry is also relevant to *non*-visual localization of objects relative to the *eyes*: the brain can use information about head motion, for instance from the otolith organs, to compute the changing locations of unseen objects relative to the rotary centers of the eyes (Blakemore and Donaghy 1980; Viirre et al. 1986, Medendorp et al. 2000). That computation takes into account the relative locations of the eyes' and head's axes, so the principles of linkage geometry we have studied here are also relevant to other tasks besides visual localization.

Range effects in computational networks

Our interpretation of the systematic misreaching when gaze is off-target is that it is a sign of incomplete learning. The brain's networks are shaped by learning, so we should expect their computations to be finely calibrated for well-practiced tasks and not so well calibrated for uncommon tasks, outside the network's normal range of experience. In our brains, it is plausible that the visuomotor system is calibrated very well for Gaze-On-Target reaching and less well for Gaze-Off-Target reaching (Pelz et al. 2001). Of course there are many different ways that the network's computations might become uncalibrated. We know that miscalibrations in the visual system lead subjects to mislocate targets seen in the peripheral retina (Bock 1986; Enright 1995; Henriques et al. 1998; Henriques and Crawford 2002; Medendorp and Crawford 2002; Pouget et al. 2002). Other possible miscalibrations might conceivably turn the gaze point into a magnet; that is, they might cause the network to give undue weight to the fixation point when it estimates target locations. For well-practiced tasks like Gaze-On-Target reaching the magnetic effect might not be present at all, or it might be too small to detect because it is drowned out by noise. In short, the inaccuracy of Gaze-Off-Target reaching is to be expected, given the inevitably imperfect calibration of neural networks in the brain; a magnetic gaze point might be part of this miscalibration, but there are many other possibilities as well.

A similar effect would explain our subjects' performance when they reached with the head in eccentric positions. They corrected for head orientation quite well in the Gaze-On-Target task, but less well in the Gaze-Off-Target task. So they were capable of the complex geometry involved, though again the computations were better calibrated for the more common task. Years of motor learning may be necessary for the brain to shape a computational network sophisticated enough to represent the complex eye–arm linkage with its multiple, mobile centers of rotation. And the network must be recalibrated whenever that linkage changes. In teenagers, for instance, a growth spurt may make the network temporarily out of date, and may explain their clumsiness. It is likely that some aspects of the computation, for rare tasks or ones where extreme precision is not needed, are never perfectly calibrated.

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