Exp Brain Res (1999) 126:19–30

RESEARCH ARTICLE

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Reaching beyond reach

Received: 1 October 1998 / Accepted: 7 January 1999

Abstract The analysis of errors in two-joint reaching movements has provided clues about sensorimotor processing algorithms. The present study extends this focus to situations where the head, trunk, and legs join with the arm to help reach targets placed slightly beyond arm's length. Subjects reached accurately to touch "real targets" or reached to the remembered locations of "virtual targets" (i.e., targets removed at the start of the reach). Subjects made large errors in the virtual-target condition and these errors were analyzed with the aim of revealing the implications for whole-body coordination. Subjects were found to rotate the head less in the virtual-target condition (when compared with accurate movements to real targets). This resulted in a more limited range of head postures, and the final head angles at the end of the movements were geometrically related to the incorrect hand locations, perhaps accounting for some portion of the errors. This suggests that head-eye-hand coordination plays an important role in the organization of these movements and leads to the hypothesis that a representation of current gaze direction may serve as a reference signal for arm motor control.

Key words Motor control · Arm movement · Reaching · Posture · Gaze · Hand-eye coordination

Introduction

Imagine reaching out to touch something that is slightly beyond arm's length. In this case, the whole body becomes part of the reaching movement. A small step and a slight bend of the trunk are readily incorporated into the arm movement, such that reaching with a moderate amount of body movement feels at least as natural as the simpler case of reaching from a stationary body. However, with a step and a bend, the arm movement cannot proceed from a stationary base of support, and it is difficult to conceive of its planning and control in a stationary frame of reference. In addition, eye-hand coordination is more complex than in the case of a stationary head and body. Understanding the basic organization of this eye-hand-body coordination was the aim of the present study.

Arm/trunk/leg coordination has recently been studied in the context of bending and reaching movements (Pozzo et al. 1998; Thomas et al. 1998). In earlier work, Pozzo and Berthoz analyzed a wider variety of locomotor and acrobatic tasks and postulated that the neural control of the head movement plays a key role in trunk/leg coordination (Pozzo et al. 1990, 1992, 1995). Exploring tasks ranging from walking to backward somersaults, these investigators discovered periods of stabilization of the head *in space*, with the body moving about in the meantime. This suggested that head placement and stabilization (perhaps using vestibular/gravity information) provides a stationary frame of reference (an "inertial guidance platform") for the coordination of the many body segments. Periods of angular head stabilization can also be observed and appreciated in artistic and gymnastic exhibitions (e.g., in dancers, divers, and figure skaters), making this idea of the head as an inertial guidance platform an attractive and intuitive hypothesis for complex motor control.

Do head placement and stabilization also dictate the control mechanism for the coordination of stepping and reaching movements? A relatively large amount of effort has been devoted to studying reaching movements of the arm only, with a stationary head and body (reviewed by Georgopoulos 1986, 1991; Jeannerod 1988; Milner and Goodale 1995). Many of these studies employed a paradigm where the subject fixed his or her gaze on a stationary target prior to and during the reach. In some of these studies, the investigators implemented an experimental

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situation called the “virtual target” condition, where subjects looked at the target, remembered its location while the lights were extinguished and the target was removed, and then attempted to place the tip of a small pen on this exact spot (e.g., McIntyre et al. 1997; Vindras and Viviani 1998). In the study of Soechting and Flanders (1989), although all of the virtual target locations were well within reach, subjects missed the most distant targets by as much as 10 cm (they under-reached, reporting a location proximal to the target). The analysis of the errors in this virtual-target condition gave rise to a model of visuomotor transformation with eye-, head-, and shoulder-centered frames of reference all fixed to the stationary body (Flanders et al. 1992). In the present study, we used a similar experimental approach, but obtained a different result: instead of under-reaching as in the case of the stationary body, subjects reached too far when the reach also involved a step. Interestingly, the error in hand placement was associated with a different strategy for head movement (when compared with an accurate step and reach to a visible target).

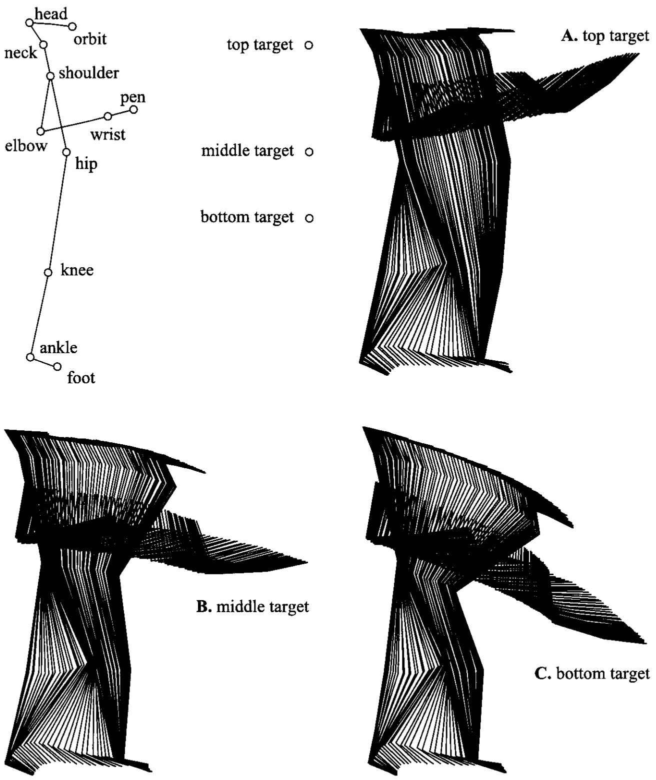

Fig. 1A–C Human stick figures illustrate simultaneous stepping and reaching movements. Examples are shown for three target locations: top (**A**), middle (**B**), and bottom (**C**). In the *upper left-hand corner*, we show a single stick figure at the standard initial posture. This posture represented each subject’s most comfortable stance, with the elbow flexed just enough to avoid obstruction of the hip marker. The line on the head was 18 cm. The foot started and ended flat on the floor

Materials and methods

Experimental design

Overview. The first of the two experiments was designed to observe subjects’ whole-body configuration during movements to a wide range of locations (52 targets). In each case, the target was distant enough that the most natural way to reach it involved taking one step. During one block of trials, the subject reached to a remembered target location (“virtual target”), and, during a second block of trials, the subjects moved accurately to touch a visible target (“real target”). In the next experiment, we followed up on the initial results using a small subset of the locations (three targets). This permitted the use of repeated trials to the same target to allow a binary comparison of fast versus slow movements and movements to virtual targets with eyes open versus eyes closed. Because the 3-target experiment was simpler than the 52-target experiment, it will be described first in the sections below (under “Reaching to three targets”) and in the results section.

General experimental conditions. At the start of each trial, the subject stood in a standard initial posture (see Fig. 1) with his or her feet in a starting position marked on the floor. Reflective markers were placed on the body, as shown in Fig. 1. We adopted the conventions of Pozzo and colleagues (1990) for marker placement with the following exceptions: (1) the shoulder marker was over the belly of the medial deltoid instead of on the acromion,(2) the line indicating the Frankfort plane was extended by attaching an 18 cm dowel (with markers at both ends) to the subject’s head, and (3) the subject held a 17 cm long pen in his or her right hand, which in most cases had a reflective marker at the tip. All targets were placed in the subject’s mid-sagittal plane and the subject stepped with the right foot and reached with the right arm. The movements were video-taped at 60 Hz and marker locations were digitized using a system from MotionAnalysis. For the 52-target experiment, we used one camera, calibrated in the plane of the targets; for the 3-target experiment, we used two cameras and calculated positions in three dimensions.

The procedure was approved by our Human Subjects Committee and all (six) subjects were normal and gave informed consent. The subjects ranged from 1.75 m to 1.84 m in height and from 20 to 52 years of age. All reported that they were right handed. Five subjects took part in the 52-target experiment (three females and two males). We initially expected the subject to reach short of the target, instead of over-reaching, and the first subject (subject 0, a female) surprised us with this result and often bumped into the target. Therefore, this first data set could not be used, and we subsequently reprogrammed the target placement (see below) for the next four subjects (subjects 1–4). For the 3-target experiment, we used two of the same subjects as in the first experiment (subject 1, male, and subject 2, female) and enlisted one new subject (subject 5, male).

Reaching to three targets. Subjects stepped and attempted to place the penpoint on one of three target locations, all in the subject’s mid-sagittal plane at a constant distance from the subject’s initial body axis (90 or 100 cm, depending on the height of the subject). The vertical coordinates of the target locations were determined separately for each subject: the top target was at the level of the neck marker (cervical vertebra C7, Fig. 1A); the middle target was at the level of the hip marker (Fig. 1B); the bottom target was at a level half-way between the hip and knee markers (Fig. 1C).

On each trial, one target was presented by the experimenter; it consisted of a fishing sinker (2.5 cm diameter) hung from the ceiling with wire. The subjects stepped, reached, and closed their eyes (when appropriate) immediately upon hearing an audio tone. For each target location, there were several possible instructions. The subjects might be asked to move either fast (about 1 s movement time) or slow (about 2 s movement time). Also, the subject might move accurately to a real target with eyes open, or might be asked to remember a virtual target location and move either with eyes open or eyes closed. In these virtual target conditions, the experimenter also reacted immediately to the tone (i.e., with an auditory reaction time) by grasping the target and removing it forward and to the right. Thus, subjects did not see the target move in the eyes-closed condition. The subjects were aware that each target was in one of only three locations. Subjects were asked to hold the final posture for 1 s before returning to the starting posture.

The various trial types are summarized in the lay-out of the data in Fig. 2: (1) top real target/eyes open; (2) middle real target/eyes open; (3) bottom real target/eyes open; (4) top virtual target/eyes open; (5) middle virtual target/eyes open; (6) bottom virtual target/eyes open; (7) top virtual target/eyes closed; (8) middle virtual target/eyes closed; (9) bottom virtual target/eyes closed. There were five repeats of each of the 18 trial types (nine fast + nine slow) for a total of 90 trials. The presentation order was randomized.

Reaching to 52 targets. For this experiment, we programmed a robot (model TCM, UMI Microbot) to place a target (a sphere 2 cm in diameter) at one of 52 locations on each trial. The locations were approximately 1 m (±25 cm) anterior to the subject's starting position and ranged over approximately 1 m in the vertical dimension (see Fig. 4). Each location was visited only once and the various locations were covered in a pseudorandom order on successive trials. The subject was instructed to move naturally and at a comfortable pace.

The subject performed one block of 52 trials with virtual targets and then one block of 52 trials with real targets. Each trial with a virtual target proceeded as follows: First, the robot stopped at a target location. An audio tone then served as the cue for the subject to close his or her eyes and immediately step and attempt to place the pen tip on the remembered location. At the same time, the robot removed the target about 20 cm to the left to avoid giving the subject tactile feedback. The subject was instructed to hold the final posture for 1 s before initiating a return movement. The eyes were reopened only at the end of the return movement, and, by this time, the robot was well on its way to the next target location. Thus, the subjects received no information regarding the accuracy of the movement. Each trial with a real target proceeded similarly except that the eyes remained open, the target was not removed, and the subject could touch the target with the pen tip. (However, as in the 3-target experiment, subjects generally stopped just short of and to the right of the target to avoid hitting it.) As in the 3-target experiment, all subjects were asked to foveate the real target throughout the movement.

Data analysis

For each trial, we created a stick-figure representation, as shown in Fig. 1, calculated the tangential velocity profile of the wrist marker (Fig. 2), and plotted joint and segment angles as a function of time. The wrist tangential-velocity profile was examined to determine the frame number corresponding to the end of the movement, and this point in time (defined as the point where the speed returned to the base-line level) was identified visually using horizontal and vertical cursors. The steady-state or "final" values for various parameters were then computed by averaging the values associated with the next five frames. The tangential velocity profile was also used to identify unusual trials, where the subject made a second movement at the end, paused, or stepped twice. Such disturbances typically resulted in a bimodal velocity profile, and, based on this exclusion criterion, we discarded about 5% of all trials from further analysis. Approximately 2% of the trials were excluded due to technical difficulties associated with the digitization of the marker locations.

For the 3-target experiment (where we had five repeats of each of 18 conditions), we used analysis of variance (ANOVA, with Scheffé post-hoc testing), or Student's *t*-testing when appropriate. For the other experiment (where we had 52 target locations for 52 trials), we mainly relied upon linear regression statistics. The analysis was performed in LabVIEW and SYSTAT software packages.

Results

The main results involve an interpretation of the sources of the errors in hand placement observed in the situation where the target was remembered (virtual target) instead of physically present (real target). We begin by describing general aspects of the whole-body movement that were characteristic of all subjects and seen in both experiments. We will then present a more detailed account of the specific results of the two experiments.

General characteristics of reaching with stepping

The act of reaching to targets slightly beyond reach displayed many of the well-known features of targeted arm movement. The stick figures in Fig. 1 show that the whole body advanced with one fluid motion. A stick figure was drawn for each frame (every 1/60 s) so that the spacing of the figures reveals gradually faster and then slower movement. This smooth increase and decrease in speed is consistent with "bell-shaped" tangential velocity

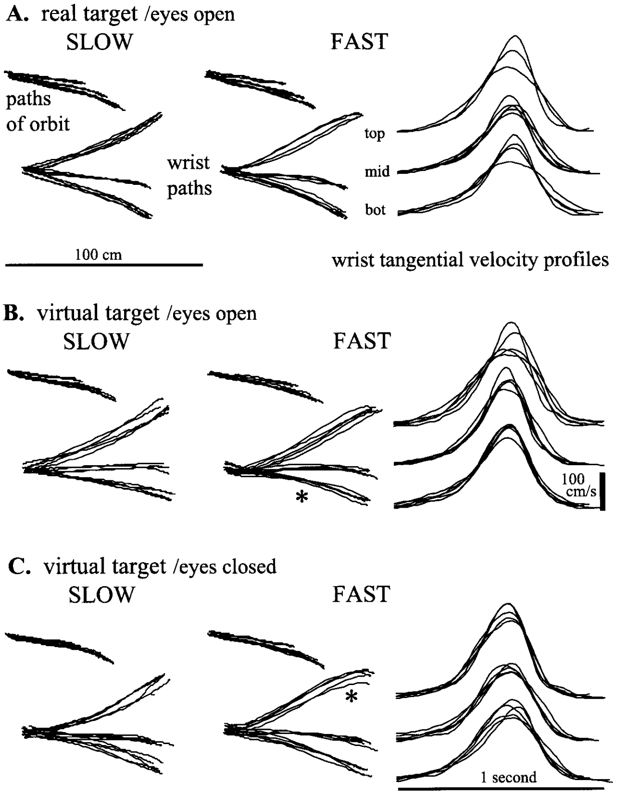

Fig. 2A–C Spatial paths of the marker on the orbit and the marker on the wrist for five movements to each of three targets in each experimental condition. Cases where fast versus slow comparisons revealed significantly different curvatures are marked (*). The tangential velocity of the wrist marker typically followed a bell-shaped profile. Using examples from subject 5, this figure exhibits similar profiles for the various experimental conditions: **A** real target/eyes open, **B** virtual target/eyes open, **C** virtual target/eyes closed. The profiles from trial repetitions are aligned to show the similarity in shape and do not begin exactly at time zero. *top* Top target, *mid* middle target, *bot* bottom target

Table 1 Peak tangential velocity (cm/s) of the wrist marker (±SEM) for *n*=5 trials. The various experimental conditions were: real target/eyes open (*r/o*), virtual target/eyes open (*v/o*), and virtual target/eyes closed (*v/c*). Target locations were top (*top*), middle (*mid*), and bottom (*bot*)

Condition	Subject 1	Subject 2	Subject 5
r/o top fast	257 (9)	172 (7)	232 (18)
v/o top fast	267 (8)	178 (4)	232 (18)
v/c top fast	259 (11)	160 (4)	236 (10)
r/o top slow	116 (4)	125 (7)	120 (7)
v/o top slow	106 (7)	108 (3)	128 (5)
v/c top slow	112 (3)	105 (3)	115 (3)
r/o mid fast	261 (8)	165 (4)	190 (9)
v/o mid fast	289 (4)	175 (6)	232 (17)
v/c mid fast	267 (7)	154 (4)	198 (5)
r/o mid slow	109 (4)	105 (4)	104 (3)
v/o mid slow	120 (6)	103 (2)	105 (3)
v/c mid slow	102 (2)	102 (4)	100 (7)
r/o bot fast	257 (12)	184 (6)	185 (14)
v/o bot fast	291 (14)	173 (6)	221 (7)
v/c bot fast	245 (12)	180 (12)	198 (8)
r/o bot slow	118 (3)	121 (3)	108 (3)
v/o bot slow	136 (7)	123 (3)	108 (4)
v/c bot slow	132 (4)	115 (3)	104 (3)

profiles, one of the hallmark features of reaching movements (e.g., Atkeson and Hollerbach 1985). Figure 2 exhibits the tangential velocity profiles of the wrist marker for the various experimental conditions of the present study. The velocity profiles in Fig. 2A are from accurate movements to real targets, whereas the profiles in Fig. 2B and C are from movements to virtual targets. We did not perform a detailed analysis of the shape and symmetry of the velocity profiles. However, since the velocity profile is a sensitive assessment of the basic form of the movement, we were interested in a qualitative comparison of profiles associated with the different experimental conditions. As shown in Fig. 2, the various experimental conditions did not result in noticeable differences in the overall form of the wrist transport. The peak tangential velocity of the wrist marker was approximately 200 cm/s for fast movements and 100 cm/s for slow movements and showed no consistent differences between movements to virtual and real targets (Table 1).

Reaching to three targets under various conditions

With this two-fold difference in movement speed, we were in a position to test the hypothesis that faster movements followed different trajectories and were associated with a different pattern of errors in the virtual-target conditions. Figure 2 shows the paths of the orbit marker and the wrist marker for each target and each experimental condition. We used a standard index of path curvature to compare the fast versus slow arm movements (maximum perpendicular deviation from straight path/length of straight path, Atkeson and Hollerbach 1985). Of the 27 fast/slow pairs (three targets × three conditions × three subjects), we found significant differences in only three cases (*t*-test, $P<0.05$). Two of these are marked by asterisks in Fig. 2: for subject 5 in the virtual target/eyes open condition, fast movements to the bottom target were significantly more curved than slow ones, and for the top target in the virtual target/eyes closed condition the curvatures of fast and slow movements were opposite in sign. Subject 1 showed a significant difference only for the top target in the virtual target/eyes closed condition, and for subject 2 this was the only condition were the comparison approached statistical significance ($P=0.06$). Wrist paths for fast versus slow movements were never significantly different in the real-target condition. Thus, we can conclude that, despite the dramatic increase in dynamic torques associated with the faster movements, the coordination of the arm and body is such that hand path is generally speed invariant (as previously shown for arm movement with a stationary body: Atkeson and Hollerbach 1985; Soechting and Lacquaniti 1981).

We also tested whether fast and slow movements were associated with different endpoint errors. Using an ANOVA including all of the subjects and conditions (see Methods), we identified a small but significant ($P<0.05$) difference between the errors in hand location for fast and slow movements: the hand location at the end of a fast movement was on average 1 cm farther forward and 1 cm lower than for slow movements. This is shown in Fig. 3A, where the boxes represent the average ± standard error of the final hand positions. This fast (thick lines) versus slow (thin lines) difference is quite small compared to the overall magnitude of the errors in the virtual target conditions (i.e., the black boxes representing real targets vs. the open or shaded boxes representing errors in reaches to virtual targets). Although reaches to virtual targets ended significantly farther forward than reaches to real targets ($P<0.001$), the eyes-open versus eyes-closed virtual target conditions could not be distinguished along this dimension ($P>0.05$). However, hand placement for virtual targets with eyes open was on average 5 cm higher than with eyes closed, and 6.2 cm higher than for real targets (both $p<0.001$).

In Fig. 3B, we show a horizontal perspective of the average hand locations for all subjects and all conditions. Anterior to the body is up in this figure, and it is apparent that both virtual target conditions (open circles for eyes open and filled circles for eyes closed) were associated with errors in over-reaching (compared with the hand placement for real targets, square symbols). This figure also shows that, with the eyes closed, the hand was placed about 3 cm to the right of the location chosen with the eyes open (ANOVA, $P<0.001$). This is consistent with previous results showing that virtual-target errors shifted to the right for movement of the right arm in the dark compared with movement in the light (Soechting et al. 1990).

In the sections below, we will consider several possible explanations for the overshoot errors seen in the virtual target condition. However, before moving from the

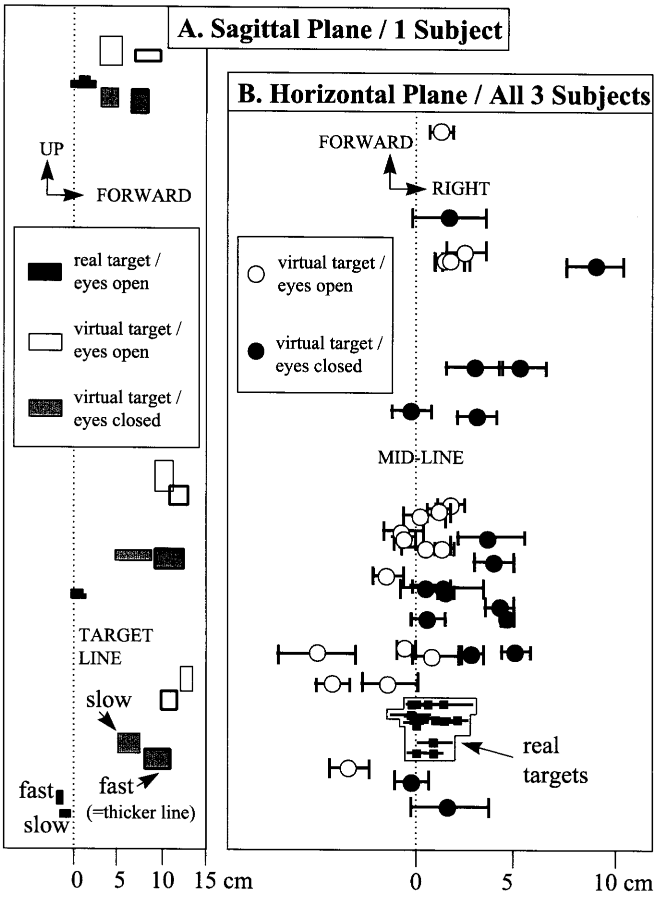

Fig. 3A, B Errors in placing the tip of a hand-held pen on the remembered location of three different targets. **A** Sagittal-plane view, subject 5. Each *box* delimits the standard error of the mean pen placement in the two dimensions (*thicker lines* represent the faster movements). **B** Horizontal-plane view, subjects 1, 2, and 5. For subjects 1 and 2, the real target locations were 100 cm anterior to the initial body axis; for subject 5, they were 90 cm distant. Both plots show that reaches to virtual targets (*open symbols* for eyes open, *filled symbols* for eyes closed) overshot reaches to real targets (*square black symbols*). The horizontal view in **B** shows that errors with the eyes open tended to be centered on the subjects' midsagittal plane (*dashed line*), whereas errors with the eyes closed were shifted an average of 3 cm toward the right arm (the reaching arm)

Table 2 Final head angle (±SEM) for n=5 trials (in degrees). The various experimental conditions were: real target/eyes open (*r/o*), virtual target/eyes open (*v/o*), and virtual target/eyes closed (*v/c*). Target locations were top (*top*), middle (*mid*), and bottom (*bot*)

Condition	Subject 1	Subject 2	Subject 5
r/o top fast	–1.2 (1.0)	6.1 (1.6)	3.6 (0.6)
v/o top fast	–3.0 (1.0)	6.4 (1.7)	6.4 (0.6)
v/c top fast	–9.3 (0.9)	2.3 (1.0)	4.3 (0.7)
r/o top slow	–4.0 (0.7)	2.2 (0.9)	3.2 (0.2)
v/o top slow	–6.6 (1.5)	6.3 (1.4)	6.5 (0.9)
v/c top slow	–7.0 (1.4)	2.1 (1.8)	3.6 (0.4)
r/o mid fast	–22.1 (1.5)	–9.5 (1.7)	–15.8 (1.0)
v/o mid fast	–21.5 (1.4)	–1.8 (0.4)	–6.7 (0.3)
v/c mid fast	–18.2 (1.8)	–1.2 (2.0)	–5.6 (0.6)
r/o mid slow	–21.7 (1.0)	–16.2 (2.7)	–17.0 (1.3)
v/o mid slow	–17.8 (1.6)	–1.9 (0.4)	–7.3 (1.0)
v/c mid slow	–18.9 (1.1)	–2.1 (1.6)	–5.7 (0.9)
r/o bot fast	–31.9 (1.1)	–21.0 (0.5)	–23.9 (0.6)
v/o bot fast	–33.1 (2.3)	–12.3 (0.8)	–14.2 (0.9)
v/c bot fast	–31.5 (1.1)	–8.4 (2.4)	–11.6 (0.5)
r/o bot slow	–33.0 (1.8)	–24.7 (0.4)	–25.9 (1.1)
v/o bot slow	–34.2 (1.2)	–12.1 (1.9)	–14.0 (0.5)
v/c bot slow	–35.5 (1.4)	–8.8 (1.4)	–10.3 (0.6)

3-target experiment to the 52-target experiment, we note that Fig. 2 qualitatively shows a result that we will pursue in more detail: the path of the marker on the orbit was more stereotypical for movements to virtual targets than for movements to real targets. For example, the paths for slow movements to real targets show a marked gradation, depending on the target location (Fig. 2A), whereas the paths for the comparable set of movements to virtual targets (eyes closed) are superimposed (Fig. 2C). We also found that final head angles for real targets could be reliably distinguished from head angles associated with the virtual-target eyes-open and eyes-closed conditions, but that the two virtual-target conditions were more difficult to dissociate statistically (Table 2). For subject 1, this real target/virtual target difference was significant only for the top targets, whereas subjects 2 and 5 showed the largest difference for movements to the middle and bottom targets. In the experiment described below, we circumvent this type of inter-subject variability by considering a larger range and a much larger number of target locations. The design of the following experiment was also preferable, in that the subject moved only twice (once in the block of virtual targets and once in the block of real targets) to each of 52 targets and, therefore, could anticipate neither the correct direction nor the correct distance.

Errors in reaching to 52 virtual targets

Based on previous work (Flanders et al. 1992), we initially expected that subjects would fall short of the virtual targets, missing them by as much as 10 cm. Instead, when subjects reached to a wide range of targets, they generally reached too far, missing by as much as 20 cm (Figs. 4 and 5). In Fig. 4, we show data from the subject with the largest errors: the spatial locations of the virtual targets are represented by open circles, and the arrowtips pinpoint the location indicated by the subject's placement of the tip of a hand-held pen (hereafter referred to as the hand location). Figure 5 summarizes the pattern of errors for all four subjects using a similar format: in each case the majority of the errors had forward and downward components.

In Fig. 4, the stick figures associated with one trial are included for scale (the line on the head is 18 cm long). This series of stick figures also serves to illustrate the general finding that subjects did not simply pass the hand through the target location, failing to stop in time.

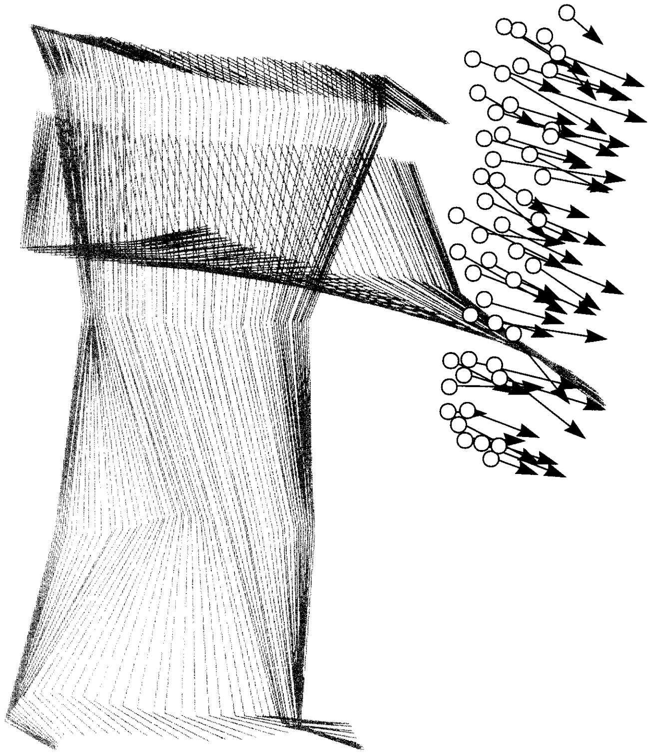

Fig. 4 The *arrows* represent errors in placing the tip of a hand-held pen on the remembered locations of sagittal-plane targets. A robot placed (and removed) a target at (from) a single location (*open circle*) in each of 52 trials. The stick figures from one trial are shown for scale; the line on the head is 18 cm long. The data are from the subject with the largest errors (subject 1)

In this trial, the hand passed above the target (compare the gray hand path to the circle/arrow pair representing its target/error); for the highest target locations, the hand passed beneath the target (path data not shown). Thus, the hand followed a different path depending on whether the target was visible or not. This rules out the idea that subjects, in the absence of visual feedback, simply failed to stop at the correct point along the usual path.

Since trials with virtual or real targets were presented in blocks, we wondered if part of the overshoot error might be due to a larger step length in the virtual-target condition. We measured the horizontal translation of the foot marker on each trial and used a *t*-test to compare the average values representing virtual and real target conditions for each subject. The result was different for different subjects, and this inter-subject variation might explain some of the individual differences in the magnitude of the forward component of the error (see Fig. 5). Subjects 1 and 4 (the subjects with large forward components) stepped significantly farther for virtual targets ($P<0.001$ and $P<0.02$, respectively); subject 3 showed no significant difference; and subject 2 (the subject with the smallest overshoot) stepped significantly shorter in the virtual target condition ($P<0.001$). Thus, step length may have contributed to the error magnitude in some subjects. Distance errors might also be associated with an overextended placement of the arm and hand relative to the head and trunk. We tested this idea by examining the final body posture at the end of each movement. For all subjects except subject 4, the final eye (orbit maker) to hand distance was significantly greater than the final eye to virtual target distance (in a paired *t*-test, $P<0.001$). Thus, it seems that the magnitude of the errors may also be associated with an over-extended placement of the arm.

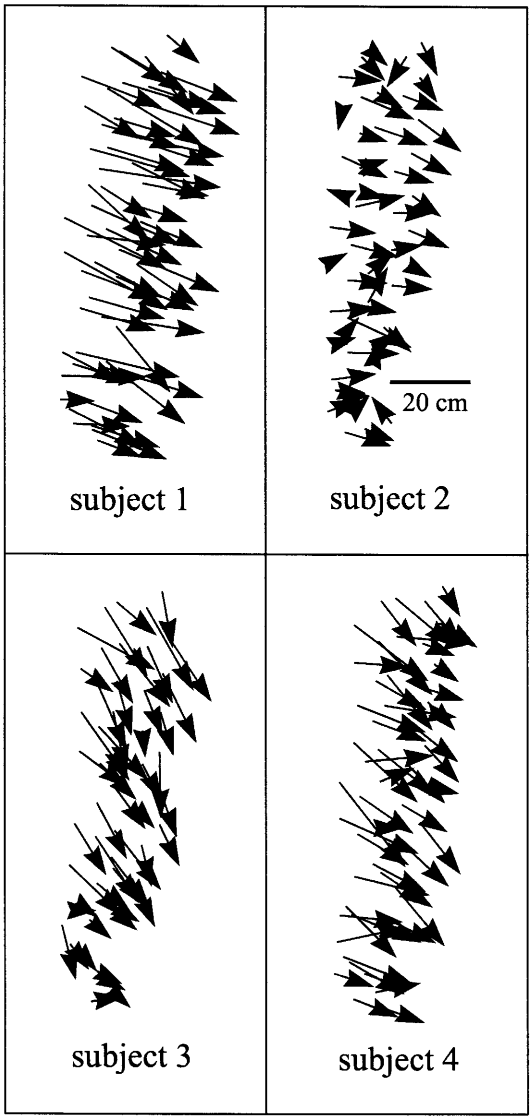

Fig. 5 A pattern of errors comparable to that of Fig. 4 was observed in all four subjects. As in Fig. 1, the *arrows' bases* represents the target locations and the *arrows' tips* represents the locations reported by the subject. In most cases, the errors had downward and forward components. Subjects 1 and 3 were males and were approximately 5 cm taller than the two female subjects

In cases where subjects stepped too far and placed the hand too far from the body, perhaps the final body configuration was appropriate for a movement to a more distant target. This would be consistent with the hypothesis that the subject misperceived the target location or that this perception was gradually distorted in memory. This hypothesis and its strictest prediction are illustrated in Fig. 6. As shown schematically in Fig. 6B to support an

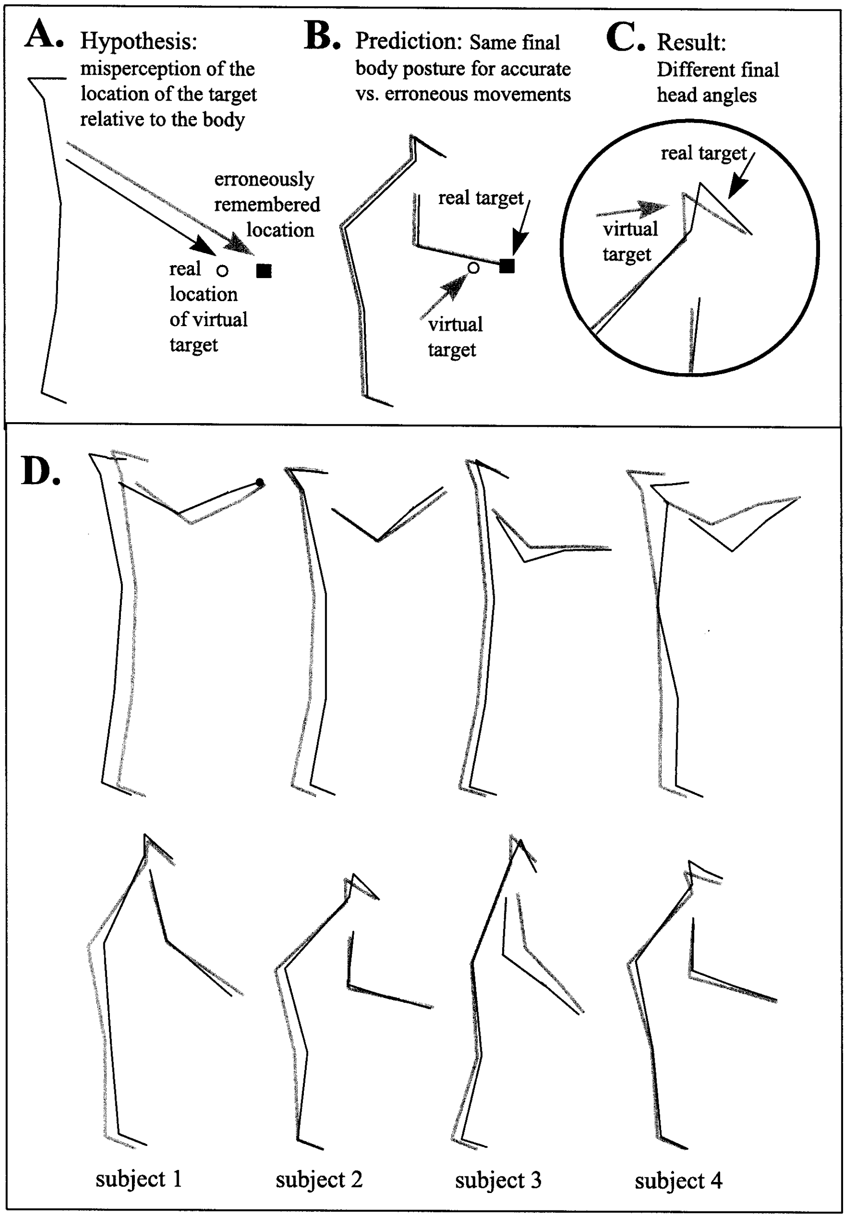

Fig. 6 **A** A misperception of the location of the target relative to the body might account for the errors in the virtual target condition. **B** An observation that would support this hypothesis would be a similarity of final body postures in the cases of: (1) an erroneous reach to a particular spatial location (*gray stick figure*), and (2) an accurate reach to the same location (*black stick figure* and *black square*). Instead, head angles differed across the two conditions, as shown for one subject (**C**) and for all subjects (**D**). The range of head angles was smaller in the virtual target condition

hypothesis involving a misperception of target location, the data should reveal that the subjects' whole-body movements to erroneous imagined locations (in the virtual-target condition) are identical to accurate movements to those same locations (in the real-target condition). We assessed this prediction by searching through our data sets for pairs of trials where the subject: (1) moved the hand to an erroneous location, and (2) moved the hand accurately to that same location. We found a total of 23 pairs where the final hand locations were within 2 or 3 cm of one another and then focused on comparing the stick figures representing the final whole-body posture at the end of these individual movements (as in Fig. 6D).

The final body configuration *did* appear to be different depending on whether the movement was to a real or a virtual target. The most prominent difference concerned the head posture (Fig. 6C): for each of the subjects, the range of final head angles (re. horizontal) was reduced in the virtual target condition, despite the similar placement of the hand (Fig. 6D). As will be shown below (in Fig. 7), the final head angle is a function of target location and ranged from zero or small, positive values (horizontal or upward, depending on the subject) to larger negative values (downward). Using the data from paired trials, we found that the virtual target condition was associated with a range reduction of 6, 14, 9, and 13° (in subjects 1, 2, 3, and 4, respectively) compared with the real-target condition. Our comparison of final body postures was somewhat qualitative due to the rather large widow of acceptance of these paired trials and the small number of pairs identified. Yet this analysis served to call strictly perceptual explanations into question and directed our attention to the influence of head position on hand placement.

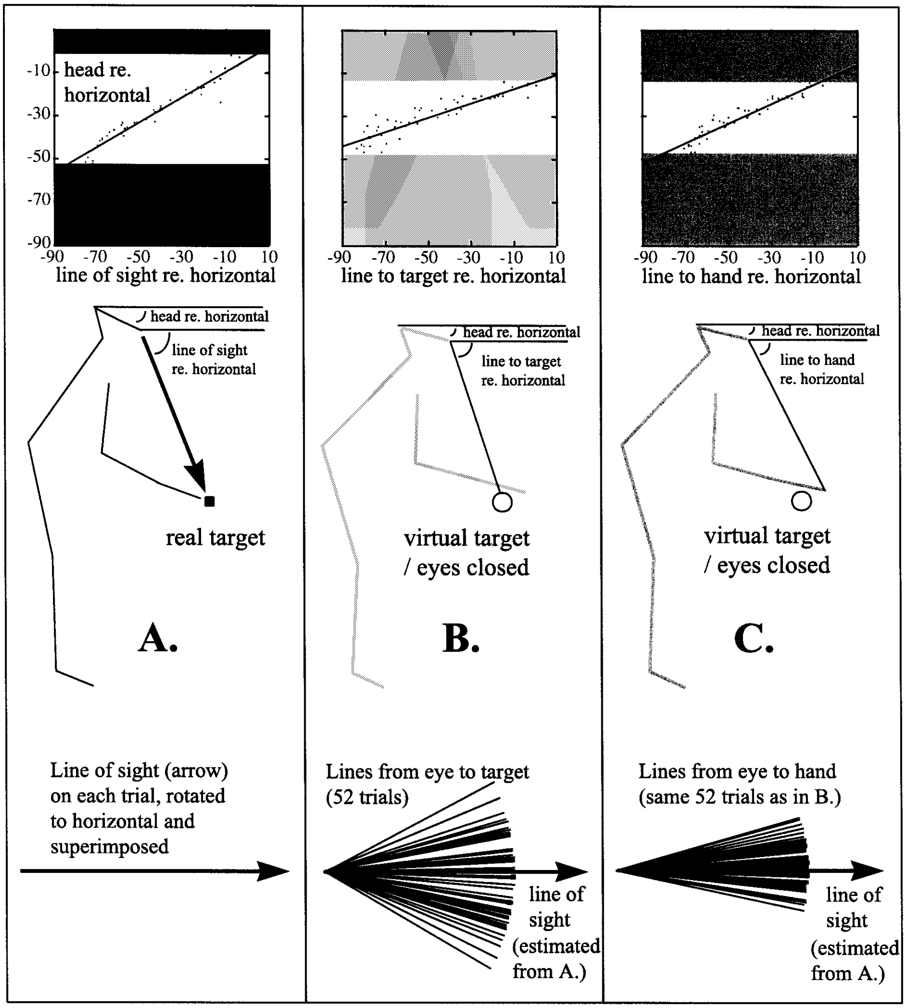

Fig. 7A–C Final head angle versus target and/or hand location. Despite the identical range of target locations, the range (*white region*) of final head angles was reduced in the virtual target condition (**B** and **C**) compared with the condition where the target was visible (**A**). The gain of the head versus target was reduced in the virtual target condition (**B**), but somewhat improved when the head angle was compared to the hand location instead of the target location (**C**). The "line of sight" was estimated by evaluating the equation of the regression line in **A** for the final head angle on each virtual-target trial. In the *bottom part* of the figure, we show the deviation from the estimated line of sight, of the line to the virtual target (**B**), or the hand (**C**)

The subsequent analysis of head/hand coupling included all of the trials (of the 52 target experiment) from all four subjects and examined the relation between final head angle and target or hand location (Figs. 7 and 8). In Fig. 7, using data from subject 1, we demonstrate that the final head angle was more closely associated with final hand location than with the virtual target location. Across the three panels, this figure compares results from the real target condition (left panel, Fig. 7A) with results from the virtual target condition (Fig. 7B and C). At the top of each panel, we show final head angle plotted as a function of target and/or hand location. As defined schematically, the target (and hand) location in Fig. 7A is expressed as the angle that the line of sight makes with the horizontal. In trials where the target was straight in front of the eyes, the line of sight was horizontal (0°) and the angle of the head was also close to 0°; for trials where the target and gaze direction was low (large, negative angles) the head angle was also low. For this subject, the gain (or slope) of the final angular relation between head and target was 0.58 and the coefficient of determination was high (r^2=0.94).

The coupling of the head to the target was diminished in the virtual target condition. As shown at the top of Fig. 7B, the gain was dramatically reduced (to 0.34), and the r^2 was also reduced (to 0.84), with an appreciable increase in scatter of the data points about the regression line. The shading on the graphs in Fig. 7A and B highlight the reduction in the range of final head postures in the virtual target conditions (despite the identical range of spatial locations for the real and virtual targets).

If one relates the final head angle to the erroneous hand location instead of to the virtual target location, there is an appreciable improvement in the gain and a slight improvement in the goodness of fit (compare the plots in Fig. 7B and C). In Fig. 7C, using data from the same 52 trials, we have replaced the angular measure of virtual target location with a comparable measure of hand location (see schematic). For this same set of final head angles, one can observe a closer coupling to the hand than to the target.

Thus, the analysis in the upper half of Fig. 7 suggests that the hand location may be closely associated with the head angle and the putative gaze direction. Although it is difficult to speak of a "gaze direction" in the virtual target condition, in the real-target condition an accurate line of sight can be computed on each trial (since the subject was instructed to foveate the target). For any arbitrary head position, the value of the gaze direction can then be predicted from the regression equation for the line in

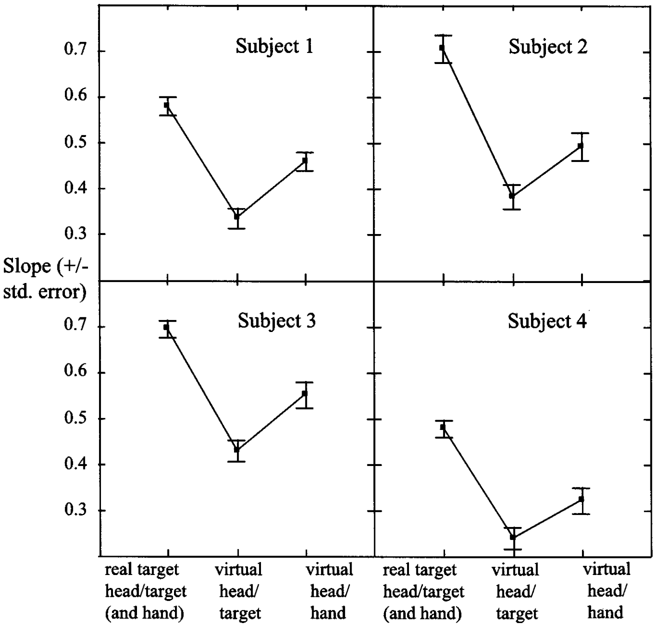

Fig. 8 The slope of final head angle versus hand location in the virtual-target condition (*far right* in each panel) had a value that was intermediate between the slopes representing the other two regressions. The highest slope was for head versus target (and hand) in the real-target condition; the lowest slope was for head versus virtual target. This trend was exhibited by all four subjects. The *error bars* represent the standard errors of the slope coefficients from linear regressions such as those presented in Fig. 7

Fig. 7A. In order to visualize the target or hand position relative to the line of sight, we used this equation for *all* trials (including the virtual-target trials) and then rotated the *estimated* line of sight to the horizontal (the arrows in the bottom half of Fig. 7). In Fig. 7B, we show 52 lines representing the angle of the virtual target relative to this estimated line of sight. The angles fall across a wide range, and, for the majority of the trials (including the posture shown in the schematic), the line to the target falls below the estimated line of sight. In contrast, when this same computation was performed using hand location, a much closer coupling was revealed (Fig. 7C).

The linear regression analysis showed that, for all subjects, the head versus hand were more closely related than head versus virtual target (Fig. 8). The tendency for the head angle to be related to the hand (or target) location was summarized by comparing the slopes of the regression lines for each case, since the slope represents the "gain" (output amplitude/input amplitude) of the head placement, or the average association between the head and target (or hand) location. As mentioned in reference to Fig. 7A, for subject 1 the slope was 0.58 for head versus target (and hand), in the real target condition. The slope dropped to 0.34 for head/virtual target, but recovered to 0.46 when these same head angles were related to the erroneous hand locations. All subjects showed the same trend for reduction across conditions and improvement when the virtual target location was replaced by the hand location. In Fig. 8, the standard error bars show the confidence limits for the slope values obtained in the linear regressions and indicate that, in all subjects, the slope of head versus hand in the virtual target condition was significantly larger than the slope of head versus virtual target, but significantly less than the slope of head versus real target. Thus, for all subjects, the gain of head/hand in the virtual target condition was intermediate between the gains associated with the other two relations.

Given the many sources of variability in placing the hand in a particular spatial location, it seems somewhat surprising that the r^2 values were undiminished when relating the head to the hand rather than the target. Since the visual information about target location presumably gave rise to the initial motor commands for the head, the body, *and* the hand, one might assume that the target and the head placement would be linked with lower variability than the head and the hand placement. Contrary to this prediction, the coefficient of determination (r^2) for head versus hand was superior in all subjects, although in some cases the difference was very small. Subject 1 showed the only statistically significant improvement, with an r^2 of 0.84 for head/target improved to 0.91 for head/hand ($F_{50,50}$=1.79, P<0.05). Subject 2 also showed a modest improvement (0.80 was improved to 0.85), despite the fact that this subject had the smallest discrepancy between hand and virtual target locations (see Fig. 5). In the other two subjects, the coefficient of determination was more comparable in the two conditions (in subject 3, 0.86 was improved to 0.88; in subject 4, 0.71 was improved to 0.73).

Since the error in hand placement appeared to be associated with the restricted range of head angles, we considered three (non-exclusive) explanations for the restricted range of head angles observed in the virtual target condition: (1) perhaps eye closure induced an unusual range of head angles due to a mechanical restriction of the eye (Bell's phenomenon) or lack of optokinetic input (Pozzo et al. 1991); (2) since the eyes were closed, subjects may have changed their postural strategy to facilitate the use of vestibular and proprioceptive inputs (McCollum et al. 1996); (3) perhaps head and eye movements are normally guided by continuous visual feedback of the target. Closing the eyes would eliminate this coordination mode and could perhaps lead to a reduction in the "gain" of the relation between the head movement and the spatial target. Although we do not rule out the first two explanations, we will present results that are consistent with the third explanation.

Since we did not record eye movements in this experiment, our data pertaining to the issue of head/eye coordination are necessarily indirect (i.e., bottom of Fig. 7). Nevertheless, the data in Fig. 9 clearly show that the subject's *head movements* followed a qualitatively different form, depending on whether his or her eyes were closed (Fig. 9A) or open (Fig. 9B). In each case, we have selected 22 trials with target locations that span the range (using data from subject 3). We then overlaid the 22 spatial paths of the marker on the orbit. Each path reflects both the translation and rotation of the head, as it proceeds during the step and reach to a different target. With

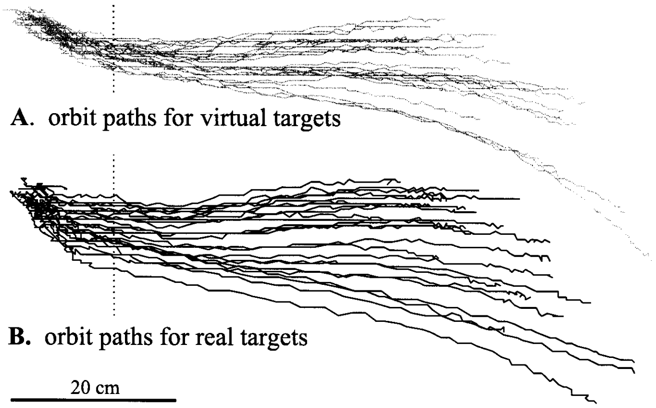

Fig. 9A, B The spatial paths of the marker placed on the orbit (see Fig. 1). Paths are shown for about half of the trials in the virtual-target condition (**A**) and the real-target condition (**B**). The paths were qualitatively different, depending on whether the eyes were closed or open (compare the range at the point indicated by the *dashed line*). In each panel, we used data from the first 15 trials and then selected seven more trials to span the range, with minimal overlap

eyes closed (Fig. 9A), the initial portions of the path nearly superimposed, and the latter portion of the paths for the lower targets seemed to reflect the bending of the trunk (cf. Fig. 1C). In contrast, when the target was visible (Fig. 9B), the paths showed a strong early dependence on the final head positions and, hence, on the target locations. The paths to the lower targets were straighter in the real-target condition.

All subjects exhibited this qualitative difference in head path between real and virtual target conditions. To quantify this apparent change in strategy, we computed (for each subject and each condition) the standard deviation of the vertical position of the orbit maker at a point in time 500 ms from the start of the movements (the approximate location of the dashed line in Fig. 9). We found that, on average, the standard deviation was 1.5× greater with eyes open (Fig. 9B) than with eyes closed (Fig. 9A) reflecting the gradation of the vertical head position depending on target position. The wider range of path heights in the real target condition reinforces the data shown in Fig. 7 regarding the range of final head angles. This shows that, throughout the reach, head movement depended heavily on the presence or absence of a visible target. Thus, our data show that the relation between head and target was reduced when the target was not visible throughout the movement.

Discussion

The results highlight the influence of vision and/or gaze on the coordination of head, body, and arm movements. Without continuous visual input, the translation and rotation of the head followed a different form (Figs. 2 and 9), and there was a significant geometric coupling between the final head angle and the erroneous hand placement (Figs. 7 and 8). As discussed below, these observations may suggest a model where a signal related to current gaze direction influences the generation of arm motor commands during the course of the movement. This idea differs from models derived from studies of reaching with a stationary body (Henriques et al. 1998; Hollerbach 1990; Paillard 1982; Pélisson et al. 1986; Soechting and Flanders 1991). In these previous models, the control was generally viewed as a single visuomotor transformation, possibly with a terminal correction based on updated visual input or feedback from somatosensation or vision of the arm or hand. Our results also extend the hypothesis (mentioned in the Introduction) that stabilization of the head *in space* provides a platform for body coordination in complex locomotor acts. We propose that stabilization of the head and eyes *on the target* normally provides a gaze-centered frame of reference for the coordination of whole-body reaching.

Multiple influences on the control of complex movements

Any motor behavior is expected to reflect a compromise of the multiple reference frames in which the relevant information is coded (Carrozzo and Lacquaniti 1994; Flanders and Soechting 1995; Soechting and Flanders 1992). We began our analysis by assessing the relative importance of several possible sources for the observed errors. We initially reasoned that the body translation must be somehow responsible for the difference between the undershooting errors observed during reaching with a stationary body and the overshooting errors observed here. We have recently come to appreciate that, even when reaching with a stationary body, kinetic constraints (such minimization of peak work) can shape the movement kinematics in predictable ways (Soechting et al. 1995). Although the additional momentum of the moving trunk *must* be a consideration in the planning and execution of these movements, the hypothesized difficulty in braking the movement did not provide a compelling explanation for the observed pattern of overshoot errors. We also entertained the hypothesis that the perceptual representation of target distance was incorrectly amended to account for the translation of the body during the step. If this were the case, one might have expected the overshoot error to diminish when additional visual information about body translation was provided by allowing subjects to keep the eyes open when moving to virtual targets. This was not the observed (Fig. 3). Furthermore, unplanned body translation is not the only source of the error, since head angle was also different in virtual target conditions (Fig. 6).

One aspect of the present results (Fig. 3B) agreed with our previous model and, in fact, replicated the results of experiments where subjects reached to virtual targets with a stationary body (Flanders et al. 1992; Soechting et al. 1990). In these previous studies, we used the directional properties of the undershooting errors to compute an hypothetical "frame of reference" for the movement control. We found that, when subjects reached in the dark or with the eyes closed, the directional errors extrapolated to the body plane at a location about halfway between the eyes and the shoulder. In contrast, when the same movements were performed with the eyes open in the light, the errors extrapolated to a point centered squarely on the eyes. Based on this result, we suggested that subjects ended the movements with a visual-feedback comparison of the hand-held pen and a remembered cue in the visual background. Given the present results, it seems equally plausible that this arm movement was continuously influenced by a tendency to align the hand with the current gaze direction (a tendency which may be stronger with eyes open).

Eye-hand coordination

There is ample evidence for a coupling between gaze control and arm movement. Perhaps the most compelling line of evidence comes from studies of tracking movements of the eyes. Several laboratories have shown that a human subject can track (with the eyes) the voluntary movement of his of her finger in complete darkness (Gauthier and Hoffer 1976; Jordon 1970; Lackner and Mather 1981; Steinbach and Held 1968). This eye tracking movement exhibits more saccades than when the same task is performed in the light, but apparently also contains a substantial slow component. Based on these results, Gauthier and colleagues (1988) proposed a model of eye and arm movement control where these two subsystems are coupled by a "coordination control center" (p. 136).

A number of related studies have shown that errors in hand pointing can be experimentally produced by mechanical deviation of the eye (Gauthier et al. 1990), vibration of neck muscles (Biguer et al. 1988; Taylor and McCloskey 1991), or vibration of arm muscles (Levine and Lackner 1979). In each case, the manipulation of somatosensory input was thought to cause a misperception of target location, and the pointing movement was viewed as a report of this misperception. However, in the case of eye and neck perturbations, the misdirection of the arm is also consistent with an hypothetical influence of gaze direction on hand placement.

A recent study by Enright (1995) provides more direct evidence for an influence of gaze direction on hand placement. This investigator asked subjects to reach and point in total darkness to various target locations. The eyes were directed: (1) toward the target (the control condition), or (2) toward a constant fixation point. As expected, there was clearly a decrement in the performance when the subjects maintained constant fixation and were not allowed to foveate the target by making a saccade to it when it first appeared. More surprisingly though, Enright found no performance decrement (relative to the control condition) in a third experimental condition where the target was never foveated, because the saccade occurred only after all the lights were extinguished (but just before the arm movement). He concluded that with or without foveal input, the orientation of the line of sight (or eye position) exerts an important influence on the control of arm movement "during the pointing process" (p. 1617).

The most unfortunate shortcoming of the present study is the lack of direct measurements of eye position. We achieved reasonable estimates of eye-in-head position during trials where subjects were instructed to foveate the target, but we were forced to estimate or speculate on the line of sight in the virtual-target condition. However, we *were* able to show that, regardless of eye-in-head position, the restricted range of the head-in-space could account for the directional errors in hand placement. These results (Figs. 7 and 8) are consistent with a model where the placement of the hand is partially biased toward the placement of the head. Assuming an angular coordinate system centered on the line of sight (Fig. 7C), this accounts for the angular component of the error, but not necessarily the distance component. In the realm of speculation, we might comment that the sign of the distance error (i.e. the *over*shoot) is consistent with an absence of ocular convergence when there is no visible target. Furthermore, the significant elevation of hand placement in the eyes-open virtual-target condition might be consistent with an hypothetical elevation of gaze direction produced by visual cues in the background (a closed wooden door about 2 m distant).

Thus, the present results would be consistent with a model where information about current gaze direction is used in the generation of arm motor commands throughout the course of a stepping and reaching movement. Our strongest evidence for this hypothesis is the coupling between errors in head and hand placement, revealed in cases when vision of the target was not available. In the absence of a visual-feedback comparison of target and hand locations, this control mechanism would necessarily rely on internal comparisons between signals related to gaze direction and arm motor commands. As suggested by Caminiti (1997), this may occur by virtue of reciprocal exchanges of information between posterior parietal areas, such as LIP and 7m (Caminiti et al. 1996; Ferraina et al. 1997), and premotor cortical areas (Boussard 1995; Graziano et al. 1994; Johnson et al. 1996). Although it is conceivable that this mechanism is engaged only when reaching involves body movement, we have also explained that one important aspect of the results of the present experiments (the bias toward the midsagittal plane with eyes open: Fig. 3B) was also observed in previous studies of reaching from a stationary body (Soechting et al. 1990).

A neuronal substrate for gaze-centered control of arm movement has recently been proposed by Anderson and colleagues (Batista et al. 1998; Buneo et al. 1998). These investigators dissociated target and gaze directions by training monkeys to reach to a given target while fixating various other targets. Reach-related activity in area 5 and in an area posterior and medial to LIP (called PRR by these investigators) was best described as being coded in an "eye-centered" frame of reference. Interestingly, in PRR, the target position was coded relative to gaze, but, in area 5, the vector of the hand path (from start to target) was coded relative to gaze.

Acknowledgements This work was supported by National Institute of Neurological Disorders and Stroke grant R01 NS27484. We thank Alan C. League for data processing and John F. Soechting for valuable discussions and comments on the manuscript.

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