Behavioral Reference Frames for Planning Human Reaching Movements

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INTRODUCTION

To plan and prepare a reaching movement, information about the position of the target and information about the current position of the hand and arm must be integrated before a motor program can be formulated that brings the hand toward the target. One inherent complexity here is how the difference vector between the position of the hand and the position of the target can be computed (Bullock and Grossberg 1988; Caminiti et al. 1998; Shadmehr and Wise 2005). This complication arises because in the respective early sensory areas, the position of the target and the position of the hand are coded in different frames of reference. For example, if the hand is not visible, its position must be derived through proprioception (Berkinblit et al. 1995). It is known that proprioceptive information about the position of the hand is somatotopically encoded along the posterior bank of the postcentral gyrus, as relative joint angles (Gardner and Costanzo 1981). When combined with information about the lengths of the various limb segments, the position of the hand in body coordinates can be computed. In contrast, there is good evidence that target location is coded in eye-centered coordinates in the early stages of movement planning, for instance, in the posterior parietal cortex (Batista et al. 1999; Medendorp et al. 2003; Prado et al. 2005). How then can the difference vector be computed given that the target location is coded in eye coordinates and the hand position encoded in body coordinates?

Conceivably, this vector can only be computed if the locations of both target and hand are presented in the same coordinate frame (Andersen and Buneo 2002; Buneo et al. 2002; Flanders et al. 1992). One scheme (see Fig. 1A) suggests that visual target locations are first transformed from eye- to body-centered coordinates using sensory signals about the linkage geometry (Carrozzo et al. 1999; Flanders et al. 1992; McIntyre et al. 1997). Subsequently, this body-centered target representation can be integrated with the body-centered location of the hand to compute the location of the target relative to the hand (Ghiardi et al. 1995; Gordon et al. 1994; Vindras et al. 2005). Hence, this scheme entails a computation of the difference vector in body coordinates.

The second scheme (Fig. 1B) proposes that the target-hand comparison—the computation of the difference vector—is done at an earlier stage of visuomotor processing, in eye-centered coordinates. Buneo et al. (2002) found neurophysiological evidence for this hypothesis in area 5, a somatomotor cortical area within the monkey posterior parietal cortex (PPC). Recently, Medendorp et al. (2005) found evidence for this scheme in the human PPC. Basically, this scheme implies that initial hand position, as derived from proprioceptive information, is transformed “backward” into eye coordinates, using eye position and other extraretinal signals. Thus this scheme implies a computation of the difference vector in eye coordinates (Buneo et al. 2002; Crawford et al. 2004).

It is not known if the two integration schemes are mutually exclusive or whether they assist each other depending on sensory conditions. For example, it is possible that the eye-centered integration scheme is deployed only when both the target location and the current hand position are simultaneously visible when planning the movement, whereas the body-centered integration scheme may be preferred when hand position must be derived from proprioceptive body-centered signals only (Andersen and Buneo 2002). The present study evaluates the two schemes with a behavioral paradigm, using the localization errors that occur when subjects reach to remembered target locations from different initial hand positions and with gaze fixed in various directions.
that the pointing targets were arranged around the center of the arm’s mechanical range. The head was oriented such that it faced the horizontal array of target light-emitting diodes (LEDs) that was placed at eye level at a distance just beyond reach. This enabled the subjects to point close to the targets with their index fingertips, without touching them, to avoid any tactile feedback about the target location. The stimulus array consisted of seven LEDs of 3 mm in diameter, separated at ~10° visual angle, with the center LED located at the central gaze direction. Each LED could be flashed in two different colors, either as a green or a red light (luminance <20 mcd/m²). During the experiments, the subject’s hand never obscured the LEDs on the stimulus array.

Prior to the experiments, we measured the location of the eyes in space and the locations of the space-fixed stimulus LEDs using an Optotrak 3020 system (Northern Digital). With this information, we were able to compute the direction of the stimulus LEDs with respect to the subject’s eyes. During the experiment, we continuously recorded the orientation of the upper arm and the location of the tip of the index finger. Optotrak data were sampled at 125 Hz with an accuracy of better than 0.2 mm and were saved on a PC for off-line analysis.

During the experiment, binocular eye movements were recorded at 250 Hz with an Eyelink II gazetracker (SR Research), which was mounted to the chair-fixed helmet. Prior to the experiment, the eye movements were calibrated by fixating the stimulus LEDs three times each, in complete darkness. This resulted in a calibration accuracy better than 0.5°. Because the head and body stayed fixed during the experiment, the orientation of the eyes within the head, as measured by the tracker, was equivalent to the orientation of the eyes in space (gaze). Rightward rotations were taken as positive.

Two PCs in a master-slave arrangement controlled the experiment. The master PC was equipped with hardware for data acquisition of the Optotrak measurements and visual stimulus control. The slave PC contained the hardware and software from the Eyelink system.

**Methods**

**Subjects**

Fifteen subjects, aged between 19 and 35 yr, gave their written informed consent to participate in the experiments. All subjects were right-handed, had normal or corrected-to-normal visual acuity, and were free of any known sensory, perceptual, or motor disorders. Subjects were tested in two different task conditions as described in the following text. Ten subjects participated in the first experiment; eight subjects performed the second experiment. All movements were made using the extended right arm. Three subjects (the authors) were familiar with the purpose of the study. They participated in both experiments. Their results were not different from those of the other subjects.

**Experimental setup**

Subjects were seated in complete darkness, with the head mechanically stabilized within a helmet construction, which was fixed to the chair. They were tested with their torso rotated 30° leftward with respect to a frontally placed horizontal stimulus array (see Fig. 2A), so...
Experimental paradigm

The experiments were designed to test the effect of gaze direction and initial hand position on the accuracy of pointing movements toward remembered locations. Using these quantitative data, we determined the frames of reference in which the pointing errors arose. We also tested whether visual feedback of initial hand position had an effect on the pattern of pointing errors. To this end, subjects were tested in two conditions, the *unseen-hand condition* and the *seen-hand condition* (Carrozzo et al. 1999). In the unseen-hand condition, subjects could not see their hand during movement planning (i.e., when the target was presented) and execution. In the seen-hand condition, visual feedback by means of a red LED on the tip of the index finger was provided from the beginning of the trial until the start of the movement. In other words, subjects simultaneously viewed the locations of the target and the hand before they executed the movement.

Both conditions were tested on different days using the same experimental paradigm illustrated in detail in Fig. 2. All trials began with the subject looking and pointing as accurately as possible to a green target, which was illuminated for a fixed duration of 2500 ms. This target could be any of the seven target locations on the stimulus array, and defined the initial position of the hand (H, initial hand position). Next, a red light was illuminated for a fixed time interval of 2000 ms, which we refer to as F (fixation point). Subjects were required to look at this light and fixate it with maximum precision, while keeping their hand directed at H. At 1000 ms after the onset of F, another green target appeared for 1000 ms, which served as the pointing target (T). Then both F and T were extinguished, instructing the subject to point at T, while still keeping gaze fixed at the remembered location of F. Subjects were instructed to point as accurately as possible to the remembered target location within a 2-s time interval. Then the next trial started, with H at a different location than the location of T in the preceding trial, to avoid any visual feedback about performance in the previous trial. Each trial lasted for 6.5 s.

During the experiment, we never tested trials in which the angular separation between F and T, or H and T, or F and H was >40° for two reasons. First, such trials may be compromised by factors such as visual acuity and spatial resolution due to peripheral vision. Second, they would constitute a subset of trials too limited to incorporate in several of our analyses. Furthermore, we did not test for trials in which T = H because this implied no pointing response. For the remaining trials, combinations of H, F and T were presented pseudorandomly. Together, this led to 204 different types of trials in the experiment, for both the seen- and the unseen-hand conditions. Subjects performed blocks of six or seven consecutive trials between which a brief rest was provided. All pointing movements were made with the extended right arm in complete absence of any visual cues. Subjects never received feedback about their performance. Before the actual measurements, subjects practiced a few blocks to become familiar with the task.

At the end of each experiment, subjects performed four pointing movements to each of the continuously illuminated targets with the room lights on to estimate the fingertip positions corresponding to pointing to their actual locations. This control also corrected for the slight offset of the marker position with respect to the fingertip. Pointing errors in the main experiments (described in the preceding text) were expressed relative to this location. For each condition (seen-hand/unseen-hand), the total experiment lasted for ~50 min.

Data analysis

Data were analyzed using Matlab software (The Mathworks). In the experiments, the torso and head were always fixed, so the head-, body-, and space-centered frames can be treated as equivalent (space = body = head). Pointing responses were converted into a degree scale by taking the polar angle of the fingertip position relative to the center of the two eyes in the horizontal plane. Final pointing positions of each movement were selected visually at the time point for which the arm had the greatest degree of stability within the 2-s pointing interval, under the requirement that the arm had correctly followed the instructions of the paradigm. A mean position was computed over an 11 sample interval (44 ms) centered at this time point. Pointing errors for a given target were computed as the displacement of the fingertip positions relative to the mean control response for that target. We excluded trials in which subjects did not maintain fixation within a 4° interval around F. Overall, typically 10 ± 8 trials (~5%) were discarded based on the arm and eye movement criteria. For the remaining trials, eye fixation accuracy was 1.7 ± 2.2° (mean ± SD). Spatial accuracy of the hand at the initial position was slightly higher for the seen-hand compared with the unseen-hand condition: 0.5 versus 1.5°, respectively.

In a further analysis, the pointing error was investigated for each of the seven body-fixed target locations—irrespective of eye or initial hand position—using a test for differences between the seen- and unseen-hand conditions. Using a multiple linear regression, we quantified the consistent changes in the error as a function of target location, the eyes’ fixation position, and initial hand position relative to the body. Based on the regression coefficients, we determined the relative contribution of each of these factors to the pointing error to identify the reference frames in which the errors arose (see Scherberger et al. 2003 for a similar analysis). For example, if the pointing error is induced in a body-centered frame of reference, there should be no contribution of either eye position or initial hand position to the pointing error. In contrast, if errors are introduced in an eye- or hand-centered stage, significant contributions of these factors could be expected. In a further analysis of the reference frames underlying visuomotor integration, we made a trial-by-trial comparison of the pointing error. More specifically, we compared the errors in two trials that have either the same respective locations of the target and hand in eye coordinates, and not in body coordinates or identical locations of the target and hand in body coordinates but not in eye coordinates. Using this pair-wise comparison, we analyzed the data of all possible combinations of trials in either the eye- or body-centered context. A correlation measure was used to test how well these reference frames could account for the data. Statistical tests were performed at the 0.05 level (P < 0.05).

RESULTS

In this study, we analyzed the errors of human pointing movements to targets at seven different locations relative to the body, executed using various initial hand positions and with gaze fixed at various directions. To start the description of the results, Fig. 3, A and B, show the distribution of the final pointing positions pooled across subjects for each of the seven target locations, irrespective of initial hand position or gaze direction. A presents the histograms for the condition in which the hand was unseen during the planning stage (unseen-hand condition); B plots the distributions when such visual feedback was provided (seen-hand condition). Pointing positions seem fairly normally distributed around each target location with the width of the distribution representing a measure for the size of the pointing errors. Statistical analysis revealed no significant deviation from normality in 11 of the 14 distributions (Lilliefors test, P > 0.05). Furthermore, averaged across the seven target locations, subjects have a tendency to be closer to the veridical position for the seen-hand condition than for the unseen-hand condition (paired t-test, P = 0.06). It also appears that the distributions are narrower for the seen-hand condition. Figure 3C confirms this observation by showing that the width of distributions (represented by their SDs) is significantly...
across the seven target locations (paired smaller for the seen-hand than the unseen-hand condition. To confirm this, Fig. 4 gaze displacement relative to the targets rather than on final as observed for these various body-fixed targets, depend on the directed 30° to the right. This suggests that the pointing errors, same as the error for the pointing target at 20° with gaze central target when gaze is deviated 10° to the right is about the direction. For example, the pointing error that occurs for a which are shifted relative to each other, depending on fixation response curves for each pointing target can be observed, they gazed to the left. Subjects pointed more correctly when the target was presented on the fovea. Furthermore, separate distributions are narrower and centered closer to the ideal points in the seen-hand condition. Final pointing positions are normally distributed around the targets in both conditions. Distributions are narrower and centered closer to the ideal points in the seen-hand condition. The difference in SD was largely independent of target location.

smaller for the seen-hand than the unseen-hand condition across the seven target locations (paired t-test, P < 0.05). Thus visual information about current hand position provided at the planning stage generally leads to greater accuracy and less variability of the pointing movements.

The question is how much of the variance in the pointing positions can be attributed to the different positions of the eyes and hand when planning the movements and how much is related to the position of the target relative to the body. We will first address this question with an analysis of the unseen-hand condition.

**Unseen-hand condition**

Figure 4 shows the systematic pointing error for the seven body-fixed target locations, averaged across all subjects, as a function of eye position. The most important observation is that subjects pointed left from the central target (0°) when they looked to the right and made rightward pointing errors when they gazed to the left. Subjects pointed more correctly when the target was presented on the fovea. Furthermore, separate response curves for each pointing target can be observed, which are shifted relative to each other, depending on fixation direction. For example, the pointing error that occurs for a central target when gaze is deviated 10° to the right is about the same as the error for the pointing target at 20° with gaze directed 30° to the right. This suggests that the pointing errors, as observed for these various body-fixed targets, depend on the gaze displacement relative to the targets rather than on final gaze direction per se. To confirm this, Fig. 4B plots the pointing errors as a function of gaze relative to the target, which indeed rearranges the data into virtually a single response curve for all seven body-fixed target locations. This observation is not uncommon or new: these pointing characteristics have been reported by various previous studies (Bock 1986; Henriques et al. 1998; Medendorp and Crawford 2002; Poljac and Van den Berg 2003).

It is important to realize that, in the preceding analysis, the initial position of the pointing hand was not taken into account. Hence the amplitude of the required movement was variable. So would the observation of a single response curve in Fig. 4B then imply that pointing accuracy is primarily related to the position of the stimulus relative to the eyes without any effect of initial hand position? We tested this in more detail by investigating the effect of initial hand position on the pointing errors, regardless of the eyes’ gaze direction. The results of this analysis, averaged across all subjects, are shown in Fig. 5. Figure 5A plots the pointing error as a function of initial hand location. Again, there are separate response curves for the various body-fixed targets, as in Fig. 4. Note that the discontinuities in the curves here are due to the task restriction that initial hand position could not be the same as the target position. As the data show, in this case the observed response curves are not flat either, but entail a substantial effect of initial hand position (or movement amplitude). In Fig. 5B, we have plotted the data as a function of hand displacement relative to the target. Again, the data points collapse into a similar error pattern for all targets, which clearly indicates that the location of the target relative to the hand has an effect on the pointing...
Following analysis, we further quantified the pointing data of the unseen-hand condition by performing a multiple linear regression to investigate how the pointing error relates to either of these factors. This approach will also enable us to disentangle the reference frame (eye, hand, body) that describes the data most parsimoniously. A similar method was used in a previous study on reference frames for target selection (Scherberger et al. 2003). We fitted the following equation

$$\text{Err} = a_0 + a_{TB}*\text{TB} + a_{EP}*\text{EP} + a_{HP}*\text{HP}$$  \hspace{1cm} (1)

to the data of each subject, with TB the location of the target in body coordinates, EP the fixation direction of the eyes (eye position) relative to the body and HP the initial position of the hand in body coordinates. In this analysis, we only incorporated those trials in which the location of the target relative to the eyes was ≤30°, to eliminate some of the nonlinearity of the response curves shown in Fig. 4B.

Table 1 lists the parameters of these fits, for each subject separately. For all subjects, we found significant correlations, 0.44 < r < 0.84 (P < 0.001 for all subjects), indicating a significant linear relationship. Parameter $a_O$, which quantifies the bias in the pointing error, was small and on average ($-0.41 \pm 0.81$, mean ± SD) not significantly different from zero ($t$-test, $P = 0.15$). Coefficient $a_{TB}$ specifies the linear dependence of the pointing error on the location of the target relative to the body, whereas parameters $a_{EP}$ and $a_{HP}$ specify the linear relationship of the pointing error with eye and hand positions relative to the body, respectively. If the target was encoded in a body-centered frame of reference, there would be no influence of either eye position or initial hand position on the pointing error, hence $a_{EP} = a_{HP} = 0$. Next, suppose if the target were encoded in an eye-centered frame of reference, which in the present one-dimensional (1-D) study is obtained by subtracting eye position relative to the body (EP) from target position relative to the body (TB). In relation to Eq. 1, it means that the effect of hand position would be zero, thus $a_{HP} = 0$, and that eye position would matter only with regard to the target, $\text{Err} = a_O + a_{TB}*(\text{TB} – \text{EP})$, hence $a_{HP} = -a_{TB}$. Following the same reasoning, we can analyze the results of Eq. 1 for the coding of the location of a target in a hand-centered frame, expressed as (TB – HP). In terms of Eq. 1, the effect of eye position could be supposed zero, $a_{EP} = 0$, and hand position would matter only with respect to the target, thus $\text{Err} = a_O + a_{TB}*(\text{TB} – \text{HP})$ and hence $a_{HP} = -a_{TB}$. To recapitulate, if errors arose exclusively in a

![Figure 5](https://example.com/figure5.png)

**Figure 5.** Effects of hand position. A: systematic pointing error, averaged across subjects, plotted as a function of hand position (i.e., hand-re-body position) for each of the 7 body-fixed target locations in the unseen-hand condition. B: data in A plotted as a function of hand displacement relative to the target, resulting in virtually 1 response curve for all 7 body-fixed target locations.

<table>
<thead>
<tr>
<th>Subject</th>
<th>$a_O$</th>
<th>$a_{TB}$</th>
<th>$a_{EP}$</th>
<th>$a_{HP}$</th>
<th>$r$</th>
</tr>
</thead>
<tbody>
<tr>
<td>S1</td>
<td>$-1.790 \pm 0.221$</td>
<td>$0.061 \pm 0.015$</td>
<td>$0.011 \pm 0.014$</td>
<td>$-0.061 \pm 0.013$</td>
<td>0.44</td>
</tr>
<tr>
<td>S2</td>
<td>$-0.856 \pm 0.267$</td>
<td>$0.123 \pm 0.018$</td>
<td>$-0.126 \pm 0.018$</td>
<td>$0.030 \pm 0.016$</td>
<td>0.59</td>
</tr>
<tr>
<td>S3</td>
<td>$-0.522 \pm 0.218$</td>
<td>$0.057 \pm 0.015$</td>
<td>$-0.069 \pm 0.014$</td>
<td>$0.004 \pm 0.013$</td>
<td>0.41</td>
</tr>
<tr>
<td>S4</td>
<td>$0.121 \pm 0.175$</td>
<td>$0.138 \pm 0.012$</td>
<td>$-0.092 \pm 0.011$</td>
<td>$-0.045 \pm 0.011$</td>
<td>0.73</td>
</tr>
<tr>
<td>S5</td>
<td>$0.521 \pm 0.278$</td>
<td>$0.243 \pm 0.019$</td>
<td>$-0.080 \pm 0.019$</td>
<td>$-0.173 \pm 0.016$</td>
<td>0.83</td>
</tr>
<tr>
<td>S6</td>
<td>$0.219 \pm 0.165$</td>
<td>$0.095 \pm 0.012$</td>
<td>$-0.073 \pm 0.011$</td>
<td>$-0.055 \pm 0.010$</td>
<td>0.64</td>
</tr>
<tr>
<td>S7</td>
<td>$-1.608 \pm 0.248$</td>
<td>$0.118 \pm 0.017$</td>
<td>$-0.116 \pm 0.017$</td>
<td>$-0.132 \pm 0.015$</td>
<td>0.74</td>
</tr>
<tr>
<td>S8</td>
<td>$-0.544 \pm 0.204$</td>
<td>$0.107 \pm 0.013$</td>
<td>$-0.030 \pm 0.014$</td>
<td>$-0.052 \pm 0.012$</td>
<td>0.66</td>
</tr>
<tr>
<td>S9</td>
<td>$0.091 \pm 0.210$</td>
<td>$0.127 \pm 0.015$</td>
<td>$-0.129 \pm 0.014$</td>
<td>$-0.017 \pm 0.013$</td>
<td>0.67</td>
</tr>
<tr>
<td>S10</td>
<td>$0.309 \pm 0.295$</td>
<td>$0.083 \pm 0.021$</td>
<td>$-0.067 \pm 0.020$</td>
<td>$-0.029 \pm 0.017$</td>
<td>0.46</td>
</tr>
<tr>
<td>MEAN</td>
<td>$-0.406 \pm 0.808$</td>
<td>$0.115 \pm 0.053$</td>
<td>$-0.077 \pm 0.043$</td>
<td>$-0.053 \pm 0.060$</td>
<td></td>
</tr>
</tbody>
</table>

Fitting Eq. 1, $\text{Err} = a_O + a_{TB}*(\text{TB} – \text{EP}) + a_{EP}*(\text{EP} – \text{HP})$, to the data of each subject in the unseen-hand condition with TB the location of the target in body coordinates, EP the fixation direction of the eyes relative to the body and HP the initial position of the hand in body coordinates. $r$: correlation coefficient of the fit. Values are means ± SD.
To the eyes and the target relative to the hand. In this case with a specific bias for some subjects to either of these frames. Body-centered target coding, with the data of 9 of 10 subjects coordinates. As Fig. 6 shows, there is little evidence for frames of reference can then be assigned three ideal points: body-centered coding (0,0), eye-centered coding (1,0), and hand-centered coding (0,1). Thus this figure allows visualizing a complete continuum of representation: eye, hand, and body coordinates. As Fig. 6 shows, there is little evidence for body-centered target coding, with the data of 9 of 10 subjects in the other zones. In other words, the data are best characterized by a mixture of eye- and hand-centered reference frames with a specific bias for some subjects to either of these frames.

If body-centered coding would play no role, the errors can be exclusively described by a combination of the target relative to the eyes and the target relative to the hand. In this case

\[
\text{Err} = -a_{\text{EP}}(\text{TB} - \text{EP}) - a_{\text{HP}}(\text{TB} - \text{HP})
\]

Relating this back to Eq. 1, it follows that

\[
a_{\text{EP}} = a_{\text{EP}} - a_{\text{HP}}
\]

Equation 3 can also be written as \( a_{\text{EP}}/a_{\text{TB}} \) versus \( a_{\text{EP}}/a_{\text{TB}} \) in a planar plot (Fig. 6). The various frames of reference can then be assigned three ideal points: body-centered coding (0,0), eye-centered coding (1,0), and hand-centered coding (0,1). Thus this figure allows visualizing a complete continuum of representation: eye, hand, and body coordinates. As Fig. 6 shows, there is little evidence for body-centered target coding, with the data of 9 of 10 subjects in the other zones. In other words, the data are best characterized by a mixture of eye- and hand-centered reference frames with a specific bias for some subjects to either of these frames.

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\]

Relating this back to Eq. 1, it follows that

\[
a_{\text{EP}} = a_{\text{EP}} - a_{\text{HP}}
\]

Equation 3 can also be written as \( a_{\text{EP}}/a_{\text{TB}} \) versus \( a_{\text{EP}}/a_{\text{TB}} \), as visualized by the black line in Fig. 6. In other words, we could expect the data points in Fig. 6 scatter around the line through the ideal (0,1) and (1,0) points. Indeed, this seems to be the case for virtually all data points. Statistical analysis across subjects also confirmed the validity of Eq. 3, showing that the sum of \( a_{\text{EP}}/a_{\text{TB}} \) and \( a_{\text{HP}}/a_{\text{TB}} \) is not significantly different from zero (paired \( t \)-test, \( P = 0.32 \)). Thus the errors observed here seem not to arise in a body-centered reference frame.

Can these data be interpreted within the visuomotor schemes outlined in the introduction? According to the body-centered integration scheme (Fig. 1A), the position of the target relative to the hand is computed by first transforming the position of the target from eye- to body-centered coordinates and then subtracting the body-centered position of the hand. Within this scheme, the present results suggest that the pointing errors arose either at the early stage (when the target is computed in eye-centered coordinates) or at the final stage (when the target is coded in hand coordinates) but not at any of the intermediate body-centered stages of this scheme. In other words, the results of Fig. 6 can be interpreted in accordance with a body-centered integration scheme by suggesting that the integration process itself is flawless, and distortions arise in the perception of the target and/or during the translation of a body-centered difference vector into joint angles. Although this is perhaps a tenable interpretation, also in theoretical terms, flawless integration may not likely be true given the extensive internal computations that are involved. In other words, it seems remarkable not to find at least some of the data in Fig. 6 in the body-centered zone if the body-centered model were correct. In this respect, the eye-centered scheme (Fig. 1B), which suggests that target and hand position are integrated in eye-centered coordinates, seems more directly compatible with the data.

Before we proceed further, recall that the reference frame analysis of Fig. 6 was based on the assumption of linearity. To make this possible, we even removed the nonlinear portion of the response from the data as shown by Fig. 4. So it can be asked whether the same results could be observed without these assumptions and simplifications. To test this, we performed the following analysis. We compared the errors of two movements taken from different experimental conditions that were identical as specified in eye coordinates but different in body coordinates and vice versa. Under the assumption that the target-hand integration is an error-prone process, a further idea behind this test is to confirm that coordinate frame that is naturally deployed in this process would predict the same pointing error for two movements of corresponding trials (Buneo et al. 2002). Using a pair-wise comparison, we analyzed all possible combinations of trials contained in our dataset in relation to the reference frame under investigation. More specifically, the eye-centered integration scheme (Fig. 1B) entails identical errors for trials that have the same locations of both target and hand relative to the eyes (as exemplified by Fig. 7B, inset). In the present 1-D horizontal case, this is the same as requiring that the errors of two movements to the same target location in eye and hand coordinates will be identical (due to co-linearity aspects in 1-D). In contrast, the body-centered integration scheme (Fig. 1A) requires identical pointing errors for trials with the same locations of target and hand in body coordinates (see Fig. 7A, inset), which is the same as comparing two movements to the same target location in hand and body coordinates. The resulting scatter plots are shown in Fig. 7, A and B, for one subject. As shown, the eye-centered integration scheme revealed a low degree of scatter (a high correlation), whereas the body-centered integration model gave a poor fit (a low correlation). In other words, this subject’s data were best described by the eye-centered integration scheme when target and hand locations were identical in eye coordinates (\( z = 4.8, P < 0.001 \) using Fisher \( z \) transformation for comparing correlations). The mean results of all subjects are given in Fig. 7C, for both the eye- and body-centered integration scheme. Statistical analysis revealed that the errors of two trials were more similar for identical movements in eye coordinates than for identical movements in body coordinates (paired \( t \)-test, \( P < 0.01 \) using Fisher \( z \)-transformed correlation coefficients). Within individual subjects, the eye-centered integration scheme produced the best description for 8 of 10 subjects.
Seen-hand condition

The results of the unseen-hand condition indicate that the pointing errors can be well described as a function of either the eye- or hand-centered location of the target or both. Errors are better accounted for by these frameworks than by a body-centered coding scheme. If these results are to be explained within the eye-centered integration scheme (Fig. 1B), they imply that the putative proprioceptive hand location signals are transformed into eye-centered coordinates in this condition. Because it is unlikely that this transformation operates flawlessly, it can be expected to add noise to the system. Accordingly, the neural computations for eye-centered hand-target integration may be more accurate if this transformation is bypassed or assisted by providing visual information about initial hand position at the moment a movement plan is being constructed (Rossetti et al. 1994). The results for the seen-hand condition, depicted in Fig. 3B, already provide justification for this idea by showing smaller distributions of pointing errors compared with the unseen-hand condition.

Figure 8 illustrates the pointing errors averaged across all subjects for the seen-hand condition. Notably, in comparison with Fig. 4B and Fig. 5B, the pointing errors are substantially smaller. The pattern of errors in A, presenting the pointing error as a function of eye orientation relative to the target, is similar to the pattern observed for the unseen-hand condition. In contrast, the effect of initial hand position is almost absent, as indicated by the nearly flat curves in B. Thus indeed, providing visual feedback of initial hand position during the planning process assists the target-hand integration process by making it more accurate and precise.

As in the preceding text, we fitted a linear model, Eq. 1, to these data to characterize the reference frames involved in more detail. This fit revealed significant correlations for each subject (0.35 < r< 0.79, P< 0.001). Table 2 displays the best-fit parameters of each subject. The bias in the pointing error ($a_0 = -0.48 \pm 0.16$) was not significantly different from the value found in the unseen-hand condition ($t$-test, $P = 0.84$). Similarly, the value of the coefficient specifying the effect of eye position ($a_{eH}$) was not significantly different between the two conditions ($t$-test, $P = 0.14$). In contrast, the seen-hand condition yielded different values for fit parameters $a_{H}$ and $a_{eH}$ than the unseen-hand condition ($t$-test, $P < 0.05$ for both parameters). Averaged across subjects, coefficient $a_{eH}$ was not significantly different from zero in the seen-hand condition ($t$-test, $P = 0.60$), implying no significant effect of initial hand position on the pointing error. Importantly, we also confirmed the validity of Eq. 3 (paired $t$-test, $P = 0.43$) for the seen-hand condition, indicating the absence of body-centered effects, which is in correspondence with the results of the unseen-hand condition.

For completeness, we also performed a pair-wise error analysis for the two transformation schemes, like in Fig. 7C. As expected, the results of this analysis, depicted in Fig. 8C, confirm that predictions of the eye-centered scheme match the
data more closely than those of the body-centered integration scheme (paired t-test, $P < 0.05$, using Fisher $z$-transformed correlation coefficients).

**DISCUSSION**

The main purpose of this study was to gain insight into the behavioral reference frames used when humans plan and execute a reaching movement. In particular, we focused on the question of how information about the position of the target and information about the current position of the hand is integrated into a motor program for a reaching movement. To investigate this, we examined the errors of human reaching movements to memorized targets located at seven different locations relative to the body. Subjects planned and executed these movements with gaze fixed at various directions and with the hand at various initial positions. Our results showed that both initial hand position and gaze direction had a significant effect on the magnitude and direction of the pointing error. We also found that the condition in which hand and target position were simultaneously visible before movement onset (seen-hand condition) resulted in smaller errors than the condition in which hand position had to be derived on the basis of proprioceptive information only (unseen-hand condition). Using a multidimensional linear fit to the data, we found that pointing errors were well described as a function of either the eye- or hand-centered location of the target or by a combination of both. Importantly, the errors did not depend on the location of the target relative to the body. The fact that making the hand visible before the movement further reduced the errors suggests that the unification of target and hand positional information is implemented at an eye-centered level, as we will further argue in the following text.

It is well known that subjects make consistent errors when asked to point to remembered targets in space. These errors were found to depend critically on visual feedback (Berkinbile et al. 1995), proprioceptive information (Hocherman 1993; Soechting and Flanders 1989a,b), eye orientation (Enright 1995; Henriques and Crawford 2002; Medendorp and Bekkerling 2000), initial hand position (Gordon et al. 1994; Sainburg et al. 2003; Vindras et al. 1998, 2005), and delay between target offset and pointing (McIntyre et al. 1998). It has also been shown that vision of the hand prior to movement initiation improves the accuracy of the movements performed (Carrozzo et al. 1999; Desmurget et al. 1997; Prablanc et al. 1979; Rossetti et al. 1994; Vindras et al. 1998). The present results are in good agreement with most of these previous studies as far as the experimental manipulations were similar. But to what extent do these errors tell us something about the internal mechanism for movement planning?

Various pointing studies have interpreted the error distributions in relation to the frames of reference used by the brain to specify the endpoint. As a result, evidence has been provided for an endpoint coded in shoulder-centered coordinates (Flanders et al. 1992; McIntyre et al. 1998; Soechting and Flanders 1989a,b; Van den Dobbelsteen et al. 2001), hand-centered coordinates (Gordon et al. 1994; Sainburg et al. 2003; Vindras et al. 2005), eye-centered coordinates (Henriques et al. 1998; McIntyre et al. 1997; Medendorp and Crawford 2002; Vetter et al. 1999), and even multiple frames of reference (Heuer and Sangals 1998; Lemay and Stelmach 2005; McIntyre et al. 1998). Lemay and Stelmach (2005) argued that the direction of a movement is coded in a frame linked to the arm, whereas amplitude of the movements is remembered in an eye-centered frame of reference. Also, McIntyre et al. (1998) argued for the separate storage of distance and direction information within short-term memory, in a reference frame tied to the eyes and the effector arm. Likewise, the present results could also be seen as evidence for two simultaneously used frames: eye-centered and hand-centered. In other words, our results are in accordance with these studies showing that more than one frame of reference is used to memorize a target location. While this explanation would be compatible with our data, another interpretation may be equally valid, using the following reasoning.

The novelty of the present study in relation to previous studies is the combined manipulation of target direction, gaze direction, and initial hand position when planning and executing a reaching movement. This crucial manipulation revealed an error pattern that allows us to put forward the following explanation of how the brain plans a reaching movement. First, the finding that the pointing errors depend on initial hand location (see Fig. 5) suggests that the brain does not specify a movement in terms of a final position (Desmurget and Prablanc 1997; Van den Dobbelsteen et al. 2001) but rather in terms of a vector (Gordon et al. 1994; Vindras et al. 1998, 2005). Conceivably, this means that target and hand locations must be expressed in a common reference frame to compute this vector. Our eye-position variations allowed us to distinguish between an eye-centered and a body-centered frame involved in this computation. We found that two movements had similar pointing errors if target and hand locations were the same in eye coordinates but not if they were identical in body coordinates (see Figs. 6 and 7). This result was found when hand and target were simultaneously visible at the planning phase but also held...
when the hand could not be seen during the planning of the movement. Therefore we can explain our results most parsimoniously by stating the brain computes a difference vector in eye-centered coordinates. But differently, our results are supportive of the view that target and hand location are integrated in eye-centered coordinates when planning a reaching movement.

Thus instead of arguing that a target location is memorized in multiple frames of reference, a theoretically equally valid and perhaps biologically more plausible interpretation (see following text) is that the brain computes a movement vector in eye-centered coordinates. One consequence of these results is that hand position must be encoded in eye-centered coordinates at the initial stage of movement planning. While this may be seen as a trivial computation when the hand is visible, for an unseen-hand it means that its proprioceptively derived body-centered position must be transformed backwards into eye coordinates. This inverse computation requires a correct incorporation of the body geometry, including information about the current orientation of the eyes, head, and shoulder, as well as stored data about the geometry of the bones and muscles in the linkage from the eyeball to the pointing hand (Henriques and Crawford 2002).

It is important to point out that the results of the regression analysis (Eqs. 1–3) are also consistent with the idea of an eye-centered hand-to-target difference vector. As this analysis showed, the final pointing response in body coordinates (P) can be described as $P = TB + Err = (1 - a_{\text{EP}} - a_{\text{HP}})TB + a_{\text{EP}}*\text{EP} + a_{\text{HP}}*\text{HP}$. These results can be rephrased within an eye-centered integration scheme, as shown in Fig. 9. As the figure demonstrates, the integration term ($\Delta P$) can be expressed as $\Delta P = TB + Err - \text{HP} = -w_{\text{HT}}*(\text{HP} - \text{EP}) + w_{\text{PT}}*(\text{TB} - \text{EP})$, with the first term of the right-hand side representing the hand position in eye coordinates and the second term an expression of the target position in eye-centered coordinates. Simple calculus then shows for their gain factors: $w_{\text{HT}} = 1 - a_{\text{HP}}$ and $w_{\text{PT}} = 1 - a_{\text{EP}} - a_{\text{HP}}$. In other words, this suggests that the systematic errors as observed in the present study can be explained by simple gain factors in the two respective pathways coding target and hand position in eye-centered reference frames. It is then also a simple matter to understand that direct visual feedback of initial hand position will improve movement accuracy by bringing the value of $w_{\text{HT}}$ closer to unity. Sober and Sabes (2003) have shown that a hand position estimate is determined by the relative weighting of both visual and proprioceptive information. Generally, vision is a more accurate sensory modality than proprioception and therefore has a greater effect on weighting. Moreover, in the perspective of this model, vision puts the hand position directly in eye coordinates, whereas a hand position based on proprioception needs an additional computation to be represented in these coordinates. Both factors likely explain the reduced errors in our seen-hand condition.

Strictly speaking, as we already mentioned in RESULTS, we cannot claim that no body-centered integration scheme can be designed that accounts for the results of the regression analysis as well. For example, suppose that the distorted target location in eye-centered coordinates is flawlessly transformed into body coordinates and then flawlessly compared with a body-centered hand position, and the movement vector is disturbed to some degree. In such a scheme, the final pointing response in body coordinates (P) can be described as $P = TB + Err = w_{\text{PM}}*(\text{TB} - \text{EP}) + \text{EP} - \text{HP} + \text{HP}$, with gain factors $w_{\text{PM}} = (1 - a_{\text{EP}} - a_{\text{HP}})/(1 - a_{\text{HP}})$ and $w_{\text{PM}} = 1 - a_{\text{HP}}$. But again, the fact that the provision of visual information about hand location improves pointing accuracy is not very supportive of the motor-distortion explanation offered by this model. We think that the collective results of both the unseen- and seen-hand conditions are much more suggestive of an eye-centered visuomotor integration scheme for the planning of reaching movements.

Why would the brain employ an eye-centered coordinate frame to compute a movement vector? One argument is that in natural daily behavior, our hands and the objects they manipulate are usually concurrently visible. This makes the use of direct visual coordinates an efficient strategy to create contingency plans for multiple potential movements (Cisek and Kalaska 2005) rather than involving the additional processing needed to establish such plans in joint-based coordinates all the time. Likewise, this may also provide the brain with a useful means to directly compute and compare the costs of various possible movements (Medendorp et al. 2005). Furthermore, in most cases not only the hand moves to the target, but so do the eyes, and an eye-centered frame may simplify this coordination (Andersen and Buneo 2002; Batista et al. 1999). A final reason for using an eye-centered coordinate frame is related to its high spatial resolution. When the eye fixates a target, the target is

![Diagram](http://jn.physiology.org/DownloadedFrom)
represented on a high-resolution scale (fovea-resolution) in an eye-centered coordinate frame. It appears that directing the eyes to an unseen-hand when executing reaches improves endpoint accuracy (Newport et al. 2001), and this could be interpreted as the map of initial arm position being retinotopic but represented less accurately for regions distant from the fovea. Resolution will deteriorate when information is transformed into body coordinates first.

We emphasize that an eye-centered movement vector by itself cannot drive the motor response. Ultimately, the brain needs to compute a joint-based movement plan for motor execution. As such, the eye-centered movement vector must be put through further reference frame transformations to convert it into joint-based or muscle-based coordinates (see Fig. 1B), requiring nonlinear operations to deal with the complex, nonlinear linkage structure between the retina and the movement effector (Crawford et al. 2004), perhaps implemented through simple gain field mechanisms (Andersen et al. 1985). In support of this, Sober and Sabes (2003, 2005) showed that a hand/arm position estimate is required at two stages of motor planning: first to determine the desired movement vector, and second to transform the movement vector into a joint-based motor command. Their results suggested that the position estimate used for movement vector planning relies mostly on visual input, whereas the estimate used to compute the joint-based motor command relies more on proprioceptive signals.

How should we interpret our findings in terms of their computational and physiological significance for the brain? The present results provide behavioral support for the eye-centered visuomotor scheme of difference vector computation as suggested by Buneo et al. (2002). These authors suggested that this kinematic comparison of hand and target information is performed at an early stage, in eye-centered coordinates, in dorsal area 5 of the posterior parietal cortex. They found neurons the firing rate of which was identical for movements for which the locations of target and hand where the same in eye coordinates (with respect to the fixation point) but different in body coordinates (with respect to the torso). We arrived at the same scheme using a similar type of analysis of the pointing errors (see Figs. 7 and 8), irrespective of whether the hand is seen or not seen during reach planning. This suggests that the brain specifies an eye-centered hand location, even if it is to be computed from proprioceptive feedback (Graziano et al. 2000). In further support of this, Battaglia-Mayer et al. (2000) have shown that cells in the parietal cortex modulate their activity depending on the location of the hand within the visual field. The present results are also in agreement with our fMRI experiments on the human posterior parietal cortex, showing that eye-centered reach representations are modulated by the effector hand (Medendorp et al. 2003, 2005).

Without doubt, the PPC is not the only region involved in computing movement vectors. For example, Stuphorn et al. (2000) have shown evidence for gaze-dependent, retinocentrically organized signals for arm movements in superior colliculus. Also, frontal regions have been claimed to play crucial roles (Boussaoud 1995; Mushiake et al. 1997), which is not surprising given the extensive parieto-premotor and/or parieto-prefrontal connections (Wise et al. 1997). Indeed, using a paradigm in which information about the target and effector is presented sequentially, Hoshi and Tanji (2000, 2004) found the dorsal-lateral prefrontal cortex and the dorsal premotor cortex (PMd) central to the process of integrating hand and target information for reach planning. It remains to be seen which of these regions, if any, have the signals at their disposal to ultimately implement the transformation from an eye-centered hand-to-target difference vector into a limb-based motor command.

To conclude, the present study clearly showed that humans make errors when pointing to remembered target locations with gaze at different directions and their arms starting from different positions. The errors could be linked to an internal mechanism that integrates target and effector information in an eye-centered reference frame rather than a body-centered frame of reference. It remains a challenge to understand how and where the central computations for a sensorimotor transformation for reaching are implemented by the brain.

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