Pointing Errors Reflect Biases in the Perception of the Initial Hand Position

PHILIPPE VINDRAS, 1 MICHEL DESMURGET, 2 CLAUDE PRABLANC, 3 AND PAOLO VIVIANI 1–4
1 Faculté de Psychologie et des Sciences de l’Education, Université de Genève, 1227 Carouge, Switzerland; 2 Department of Neurology, Emory University School of Medicine, Atlanta, Georgia 30322; 3 Vision et Motricité, Institut National de la Santé et de la Recherche Médicale Unité 94, 69500 Bron, France; and 4 Laboratory of Action, Perception and Cognition, Faculty of Psychology, Vita-Salute University HSR, 20133 Milan, Italy

Vindras, Philippe, Michel Desmurget, Claude Prablanc, and Paolo Viviani. Pointing errors reflect biases in the perception of the initial hand position. J. Neurophysiol. 79: 3290–3294, 1998. By comparing the visuomotor performance of 10 adult, normal subjects in three tasks, we investigated whether errors in pointing movements reflect biased estimations of the hand starting position. In a manual pointing task with no visual feedback, subjects aimed at 48 targets spaced regularly around two starting positions. Nine subjects exhibited a similar pattern of systematic errors across targets, i.e., a parallel shift of the end points that accounted, on average, for 49% of the total variability. The direction of the shift depended on the starting location. Systematic errors decreased dramatically in the second condition where subjects were allowed to see their hand before movement onset. The third task was to use a joystick held by the left hand to estimate the location of their (unseen) right hand. The systematic perceptual errors in this condition were found to be highly correlated with the motor errors in the first condition. The results support the following conclusions. 1) Kinesthetic estimation of hand position may be consistently biased. Some of the mechanisms responsible for these biases are always active, irrespective of whether position is estimated overtly (e.g., with a matching paradigm), or covertly as part of the motor planning for aimed movements. 2) Pointing errors reflect to a significant extent the erroneous estimation of initial hand position. This suggests that aimed hand movements are planned vectorially, i.e., in terms of distance and direction, rather than in terms of absolute position in space.

INTRODUCTION

It has been suggested that, in pointing to a visual target with an unseen hand, end-point errors reflect in part systematic biases in the kinesthetic estimation of the initial hand location (Bock and Arnold 1993; Desmurget et al. 1995, 1997; Ghilardi et al. 1995; Prablanc et al. 1979; Rossetti et al. 1995). This hypothesis has been criticized on the basis of indirect evidence (Bizzi et al. 1992; Flash 1987; for a review Desmurget et al. 1998) so that the issue remains to be adjudged. The main motivation for debating this point is the implication vis a vis the planning and control of fast aimed movements. In fact, establishing that errors in initial position affect directly end-point accuracy would contradict one influential view of movement planning: the so-called Final Position Control Hypothesis (Bizzi et al. 1992), which construes movements as transitions between stable postures and predicts that the final posture is independent of the initial one.

The present study addresses the issue directly, by comparing the end-point errors observed in a pointing task with the errors observed in a localization task in which one has to estimate the location of the unseen hand. For this strategy to be viable, both types of errors must be systematic, i.e., a simple pattern of errors must emerge when testing different regions of the workspace. Moreover, one has to demonstrate that end-point errors are causally dependent on the inaccuracy with which the initial hand position is estimated when only kinesthetic information is available. Three visuomotor tasks were designed to meet these requirements. In one condition subjects pointed to several visual targets from two starting positions without ever seeing their hand. The second condition was a control and involved again pointing to visual targets. If indeed pointing errors occur because kinesthetic sense alone cannot provide accurate estimates of the initial hand position, pointing accuracy should improve when also vision is available. Thus, in this control, subjects were allowed to see their hand until the movement started. In the third and last condition the task was to match the position of their unseen right hand with a laser spot controlled by the left hand.

As argued above, a significant correlation between initial and final postures is an argument against the Final Position Control Hypothesis. In addition, demonstrating that errors at the end of pointing movements reflect systematic biases in the estimation of the initial posture would strengthen the hypothesis suggested in previous studies (Helms Tillery et al. 1991; Soechting and Ross 1984) that common neural mechanisms are involved in estimating the hand position with respect to the body both in motor (pointing) and perceptual (matching) tasks.

METHODS

Apparatus and procedure

Ten right-handed subjects (2 males and 8 females) between 21 and 43 years of age participated in the experiment and were paid for their services. All subjects had normal or corrected-to-normal vision. They were naive about the purpose of the study. Subjects were seated comfortably in front of a digitizing table (Numonics, Montgomeryville, PA; model 2200-2436, nominal accuracy: 0.025 mm; temporal resolution: 200 Hz), inside a booth. A diffuse source of illumination could be switched off by the controlling computer, leaving the booth in complete darkness. Subjects held the movement-recording stylus with the right hand, as close as possible to
the tip. A switchable laser spot (4 mm diam) was back-projected on a translucent horizontal screen placed at 60 cm above the table. The position of the spot was controlled by the computer via a set of galvanometric mirrors. With the help of a horizontal half-reflecting mirror placed midway between the screen and the table, the virtual image of the spot appeared on the table. This arrangement prevented the arm from interfering with the spot. In two conditions (pointing tasks, see below) the location of the spot was set by the experimenter. In another condition (localization task, see below), the subject controlled the spot position with a 2-degree-of-freedom joystick held by the left hand. Two starting positions (L and R) were defined at the intersection between the table plane and the frontal plane at 26 cm from the subjects’ sternums. L and R were located symmetrically 12 cm to the left and to the right of the sagittal plane, respectively. Four sets of targets were defined, each set including 12 targets equally spaced along the circumference of a circle. Two sets were centered on point L at a distance of either 6 or 12 cm. The other two sets were centered on point R at the same two distances. In the pointing tasks, movements started either at L or R and aimed at the targets placed concentrically around the starting position. The experimenter (but not the subjects) could see the starting positions and the instantaneous stylus position on the screen of the computer. Three tasks were considered. 1) Pointing, No Vision (PNV): subjects were instructed to point as accurately as possible, with a single uncorrected movement, toward 1 of the 24 targets concentric with the starting position. Subjects could not see their hand either at the starting position, or during the movement. 2) Pointing, Static Vision (PSV): same as PNV, except that subjects were allowed to see the position of their hand at the starting position. 3) Localize, No Vision (LNV): in darkness, subjects had to use the joystick to position the laser spot in coincidence with the (unseen) tip of the stylus, which was either at L or R. Subjectively correct positioning was indicated by pressing a button on the joystick. The initial location of the spot was randomly chosen among 12 equally spaced directions at either 3 or 6 cm from the stylus position.

For all tasks, each trial involved the following steps. 1) The experimenter guided the subject’s hand toward one of the two starting positions (L or R). For LNV and PNV, the ambient light remained on until the tip of the stylus was within 4 cm from the required position. This prevented the subject from estimating visually the initial position of their hand, while at the same time, precluding proprioceptive drift (Wann and Ibrahim 1992). For PSV, the light remained on until movement onset. 2) The subject was told which task (pointing or localization) to perform in that trial. 3) The target was indicated by turning on the laser spot and the task was executed. 4) At the end of the required action (locating or pointing), the target disappeared. 5) The experimenter moved the subject’s hand by 30 cm in a random direction away from its current location, and the ambient light was turned on. Thus, subjects were never allowed to compare the hand position perceived visually with the position where (s) he thought the hand was.

The experiment was divided into two uninterrupted sessions. In the first session the subjects were tested in conditions LNV (48 localization trials: 2 starting positions × 12 spot initial position × 2 repetitions) and PNV (96 pointing trials: 2 starting positions × 24 targets × 2 repetitions). The starting position, the target, and the task were selected randomly, for a total of 144 trials. In the second session, run on a different day, the subjects were tested in condition PSV (96 pointing movements: 2 starting positions × 24 targets × 2 repetitions). The starting position and the target were again selected randomly.

Data analysis

The following analyses were performed. PNV. For each subject and each starting position, we computed the (unique) translation VT_{PNV} of all movement end points that minimized the mean quadratic error with respect to the corresponding targets (the vector −VT_{PNV} estimates the systematic component of the pointing error). Two statistical tests were performed. First, for each subject and each starting position, we tested whether the translation decreased significantly the mean quadratic error (F test). Second, Hotelling tests (multivariate test for differences in means) (Anderson 1958) determined whether VT_{PNV} was different from the null vector. Because translating all end points by VT_{PNV} is equivalent to changing the hand starting position, a significant result at either test implied that pointings would have been more accurate if the hand had started from a ‘‘virtual’’ position different from the actual one.

PNV versus PSV. As above, we estimated the systematic component of the pointing errors by the vector VT_{PSV}. It is known that vision affords only an incomplete recalibration of the position sense (Rossetti et al. 1995; van Beers et al. 1996). Thus errors in condition PSV should be reduced with respect to condition PNV, but not eliminated completely. We measured the reduction by comparing statistically VT_{PNV} and VT_{PSV} (F test on mean quadratic error and paired t-test on magnitudes).

PNV versus LNV. The perceptual error in hand location was defined as the vector from the actual hand position to the one indicated by the laser spot. For each subject and each starting position, the systematic component of this error (VP) was computed by vector averaging across trials. Three analyses tested the existence of a relation between the VP and VT_{PNV}. First, we computed between-subjects multivariate multiple regressions for each starting position (Johnson and Wichern 1982). Second, for each subject and each starting position, we tested whether the components of VT_{PNV} and VP were statistically different (Hotelling test on cartesian coordinates). Third, we examined how VP and −VT_{PNV} covaried as a function of the hand starting position (paired t-test on direction and amplitude).

In all cases the threshold for statistical significance was set at 0.05. For between-subject analyses involving 20 multiple planned comparisons (1 per subject and per starting position), the global threshold for statistical significance was corrected according to the adjustment procedure defined by Keppel (1982) (for n = 20, corrected P = 0.01).

RESULTS

PNV: end-point errors include a significant translational component

The F and the Hotelling test yielded congruent results. In 9 of the 10 subjects, and for both starting positions, adding the vector VT_{PSV} to the final position reduced significantly the mean quadratic error (MQE). The reduction ranged between 21.32 and 77.96% (48.83% on average), far beyond the mere 4.17% (i.e., 2/48) expected when the degrees of freedom of the χ² distribution are reduced from 48 to 46.

The large reduction of the MQE implies that end-point errors were systematic, i.e., independent of the movement direction and amplitude. This is illustrated in Fig. 1, which displays the pattern of errors for one subject (KA) and the average pattern for all subjects (AS). For both starting positions, most of the error vectors were of comparable magnitude and tended to be directed in a specific direction (panels KA and AS Raw data). Adding VT_{PNV} to the individual data reduced dramatically the magnitude of end-point errors (panels KA and AS Translated). The orientation of the systematic errors was not the same for the two starting positions, with errors for R being on average rotated clockwise by 42°.
FIG. 1. Mean errors before (Raw Data) and after (Translated) adding the vector VT_{PNV} to all end points. Data for all targets (filled dots). AS, average for all subjects. KA, results for the subject for whom the reduction of the mean quadratic error (MQE) was the largest. Left and right columns: data for the starting positions L and R. Note that, because of the variable direction of individual errors, averaging tends to reduce the magnitude of the bias in AS. In each panel, the systematic component of the end-point error (−VT_{PNV}) is shown as a vector originating from the starting position (the vector in the left panel is reproduced also in the right panel for comparison). For clarity, the magnitude of these vectors in panels AS has been multiplied by 2.

with respect to those for L. This rotation was robust across subjects (Fig. 2) and highly significant (paired t-test, P < 0.0001).

PNV versus PSV: viewing the hand at rest reduces the systematic errors

For all subjects, the systematic errors were much smaller in condition PSV than in condition PNV (Table 1). Across subjects and starting positions the decrease ranged from 45 to 92% (on average, 72 and 70% for L and R, respectively).

1 When the range of an angular variable is smaller than 90° and its distribution is roughly symmetrical, using the statistical formula for linear variables introduces negligible errors (Batschelet 1965).

TABLE 1. Systematic end-point errors for each subject and each starting position in the pointing task with (PSV) and without (PNV) vision of the hand

<table>
<thead>
<tr>
<th>Subjects</th>
<th>Starting Position</th>
<th>PNV, mm</th>
<th>PSV, mm</th>
<th>Variation,* %</th>
</tr>
</thead>
<tbody>
<tr>
<td>BJ</td>
<td>Left</td>
<td>21.4</td>
<td>9.0</td>
<td>58</td>
</tr>
<tr>
<td>BJ</td>
<td>Right</td>
<td>15.7</td>
<td>7.5</td>
<td>52</td>
</tr>
<tr>
<td>CP</td>
<td>Left</td>
<td>13.5</td>
<td>7.4</td>
<td>45</td>
</tr>
<tr>
<td>CP</td>
<td>Right</td>
<td>11.4</td>
<td>5.6</td>
<td>51</td>
</tr>
<tr>
<td>DC</td>
<td>Left</td>
<td>21.8</td>
<td>3.8</td>
<td>83</td>
</tr>
<tr>
<td>DC</td>
<td>Right</td>
<td>25.0</td>
<td>4.9</td>
<td>80</td>
</tr>
<tr>
<td>IC</td>
<td>Left</td>
<td>22.8</td>
<td>9.8</td>
<td>57</td>
</tr>
<tr>
<td>IC</td>
<td>Right</td>
<td>23.0</td>
<td>8.8</td>
<td>62</td>
</tr>
<tr>
<td>KA</td>
<td>Left</td>
<td>28.5</td>
<td>4.7</td>
<td>84</td>
</tr>
<tr>
<td>KA</td>
<td>Right</td>
<td>35.0</td>
<td>5.3</td>
<td>85</td>
</tr>
<tr>
<td>KO</td>
<td>Left</td>
<td>38.7</td>
<td>3.1</td>
<td>92</td>
</tr>
<tr>
<td>KO</td>
<td>Right</td>
<td>23.9</td>
<td>6.2</td>
<td>74</td>
</tr>
<tr>
<td>MO</td>
<td>Left</td>
<td>5.7</td>
<td>1.9</td>
<td>67</td>
</tr>
<tr>
<td>MO</td>
<td>Right</td>
<td>2.1</td>
<td>1.1</td>
<td>48</td>
</tr>
<tr>
<td>PL</td>
<td>Left</td>
<td>21.4</td>
<td>5.1</td>
<td>76</td>
</tr>
<tr>
<td>PL</td>
<td>Right</td>
<td>26.9</td>
<td>5.6</td>
<td>79</td>
</tr>
<tr>
<td>SM</td>
<td>Left</td>
<td>19.7</td>
<td>7.0</td>
<td>64</td>
</tr>
<tr>
<td>SM</td>
<td>Right</td>
<td>20.3</td>
<td>8.6</td>
<td>58</td>
</tr>
<tr>
<td>VS</td>
<td>Left</td>
<td>12.7</td>
<td>6.1</td>
<td>52</td>
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<tr>
<td>Mean</td>
<td>Right</td>
<td>20.5</td>
<td>6.1</td>
<td>70</td>
</tr>
</tbody>
</table>

PSV, pointing, static vision; PNV, pointing, no vision. * Error reduction due to vision.
Figure 2 compares the vectors $VT_{PNV}$ (large filled dots) and $VT_{PSV}$ (small filled dots) for both starting positions and all subjects. The difference between the amplitudes of $VT_{PNV}$ and $VT_{PSV}$ (average across subjects and starting positions: 20.6 and 5.9 mm, respectively) was highly significant (paired $t$-tests, $P < 0.0001$). As expected, errors did not vanish in condition PSV. $VT_{PSV}$ was different from the null vector (Hotelling test) in 12 of 20 cases (10 subjects $\times$ 2 starting positions).

**PNV versus LNV: motor and perceptual biases are related**

Required to indicate the position of their unseen hand with a laser spot, all subjects made consistent errors. Comparing the vectors $VT_{PNV}$ and VP (arrows in Fig. 2) shows that these perceptual errors were related to the systematic motor errors measured in condition PNV. Although both $VT_{PNV}$ and VP varied idiosyncratically, their amplitude and direction tended to be similar for any one individual. For both L and R, multivariate regression analyses demonstrated that between-subject variations of the components of $VT_{PNV}$ and VP were statistically correlated ($P < 0.001$). Moreover, for 6 of 10 subjects, the vector difference VP-$VT_{PNV}$ was not statistically different from the null vector (Hotelling test) for either starting position.

Contrasting the results across starting positions provided further evidence that $VT_{PNV}$ and VP were not independent. As mentioned above, the magnitude of the motor and perceptual errors varied from subject to subject, with |VP| being larger than |$VT_{PNV}$| in most subjects. However, for any one subject the ratio of the vector magnitudes |VP|/|$VT_{PNV}$| was not different across starting positions (paired $t$-tests, $P > 0.85$). The orientation of the motor and perceptual errors was also similar. On average, VP for R was rotated clockwise by 38° with respect to VP for L (paired $t$-tests, $P < 0.0001$). This value was not different from the one observed for $VT_{PNV}$ (42°, paired $t$-tests, $P > 0.60$).

**DISCUSSION**

We tested the hypothesis that, in the absence of visual control, position variability at the end of a hand movement reflects the variability with which kinesthesia estimates the initial position. The idea was to compare within subjects two experimental conditions, one (PNV) for measuring endpoint motor errors, the other (LNV) for measuring the initial perceptual uncertainty. The results showed that motor and perceptual errors share a common component. Indeed, movement end points to targets in the proximal workspace and perceived position of the hand were both shifted along parallel directions. The control condition PSV confirmed that seeing the hand before a pointing movement improves accuracy (Prablanc et al. 1979). Specifically, the relatively large motor errors in condition PNV suggested that kinesthesia, unaided by vision, does not provide a reliable basis for the position sense. Because localization in condition LNV was also necessarily based on kinesthetic cues, we conclude that one and the same sensory bias underlies the common error component. The analysis of the individual performances strengthened this conclusion by demonstrating a high within-subject correlation between error direction and amplitude both in the pointing and localization tasks.

The relation between the mechanisms involved in perceptual judgments and visuomotor transformations has been investigated (and, sometimes, questioned) by several experiments involving distance estimation (Gentilucci and Negrotti 1994), correction of ongoing movements (Prablanc and Martin 1992), and pointing to targets animated by illusory movements (Bridgeman et al. 1981; for a review, Rossetti 1998). Both the alignment across the workspace of the vectors $VT_{PNV}$ and VP, and the constancy of their relative magnitude support the specific hypothesis that the planning of pointing movements requires the estimation of the initial hand position, and that this information is provided by kinesthesia in much the same way as during overt perceptual estimation. It remains to be explained why the perceptual error VP tended to be larger than motor error $VT_{PNV}$. One possibility is that controlling the joystick in condition LNV involved a different, more complex visuomotor transformation than the aiming movement in condition PNV. Moreover, proprioceptive information from the hand may have drifted during the period (~5 s) necessary to position the spot (Wann and Ibrahim 1992).

The hypothesis that we favor bears directly on the ongoing debate about the control logic of the motor system in executing goal-directed movements. As mentioned in the introductory remarks, this hypothesis is difficult to reconcile with the view that the main variable controlled by the nervous system is the final position of the limb. In fact, if pointing to a spatial target were to involve a position-matching strategy, with hand displacements being planned as a succession of muscular equilibrium points (Bizzi et al. 1992), errors in the estimation of the initial hand location should not affect end-point accuracy (Desmurget et al. 1998). By contrast, the high correlation between perceptual and motor error vectors fits nicely with the alternative view that pointing movements are planned on the basis of an internal vectorial representation of the mismatch between the initial and final position of the hand (Flanders et al. 1992; Gordon et al. 1994; Vindras and Viviani 1998). Indeed, it is a logical consequence of this vector model that the inability of the nervous system to synthesize an accurate estimation of the initial hand position must be reflected in a similar bias of the movement end point (Ghilardi et al. 1995; Helms Tillery et al. 1991; Rossetti et al. 1995).

For biomechanical reasons, different patterns of motor commands are required to perform a movement with the same direction and amplitude from different initial positions. Thus errors in the perception of the initial position should not be expected to produce exactly corresponding end-point errors. Of course, it is difficult to estimate the biomechanical contribution to end-point variability. However, considering that the initial uncertainty (as estimated by VP) did not exceed a few centimeters, one would guess that this contribution is small.

**REFERENCES**


Address for reprint requests: P. Vindras, Université de Genève, Faculté de Psychologie et des Sciences de l’Education, Route de Drize 9, 1227 Carouge, Switzerland.

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