

# Vectorial Coding of Movement: Vision, Proprioception, or Both?

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## SUMMARY AND CONCLUSIONS

1. Subjects were asked to point toward visual targets without visual reafference from the moving hand in two conditions. In both conditions the pointing fingertip was viewed only before movement onset.

2. In one condition, the pointing fingertip was viewed through prisms that created a visual displacement without altering the view of the target. In another experimental condition, vision of the fingertip was not displaced. Comparison of these two conditions showed that virtually shifting finger position before movement through prisms induced a pointing bias in the direction opposite to the shift. The extent of this pointing bias was about one third of the prismatic shift applied to the fingertip.

3. Analysis of movement initial direction demonstrated that it was also less deviated than predicted from the prismatic shift. In addition, the reaction time and movement time of the reaching movement were increased.

4. This result is interpreted in the framework of the vectorial coding of reaching movement. Proprioception and vision provide two possible sources of information about initial hand position, i.e., the origin of the movement vector. The question remains as to how these two sources of information interact in specifying initial hand position when they are simultaneously available.

5. Our results are thus discussed with respect to a visual-to-visual movement vector hypothesis and a proprioceptive-to-visual vector hypothesis. It is argued that the origin of the putative movement vector is encoded by weighted fusion of the visual and the proprioceptive information about hand initial position.

## INTRODUCTION

A prominent view in motor control is that movement is encoded as a vectorial displacement in space (for discussion see Georgopoulos 1990; Jeannerod 1988). Arguments supporting this view can be found in psychophysical experiments and electrophysiological recordings in monkey. In humans, initial hand position was shown to affect pointing accuracy (Bock and Eckmiller 1986; Cruse and Brüwer 1987; Gordon et al. 1994). In addition, availability of visual information about hand position before initiation of a pointing movement improves accuracy (Desmurget et al. 1995; Elliott et al. 1991; Prablanc et al. 1979; Rossetti et al. 1994c). In monkeys, the strongest neurophysiological evidence arises from neuronal recordings of motor areas during movement, showing that the discharge patterns of motor cortical neurons are tuned to the direction of the hand movement performed in space (e.g., Caminiti et al. 1991; Fu et al. 1993; Georgopoulos 1990; Georgopoulos et al. 1982, 1986; Schwartz 1994).

If one accepts the idea of a vectorial coding, a crucial issue is how the movement vector itself is computed, and in particular how its physical origin is encoded. When aiming

at a visual target, several hypotheses can be considered about the movement vector's origin, (i.e., the hand position). First, hand position can be encoded by proprioception alone [Proprioceptive-to-visual (P-to-V) vector] or by vision alone [visual-to-visual (V-to-V) vector]. Alternately, the two modalities can both be used when the two types of information are simultaneously available [i.e., visual-proprioceptive coding of initial hand position, or visual-proprioceptive-to-visual (VP-to-V) vector]. We now consider these three possibilities (see Fig. 1).

If movements are performed in the dark, arm proprioception alone will have to be used to reach the visual target, thus using a P-to-V movement vector (P-to-V hypothesis). It is, however, unlikely that goal-directed movements are governed by a single P-to-V mechanism, because we know that pointing accuracy improves when the hand is seen shortly before movement initiation in the dark (Desmurget et al. 1995; Elliott 1988; Jeannerod 1988; Prablanc et al. 1979; Rossetti et al. 1994c; but see Ghez et al. 1990).

In patients deprived of proprioception, vision partly substitutes for proprioception (e.g., Gentilucci et al. 1994; Ghez et al. 1990; Rothwell 1982). In such cases the movement vector has to be encoded as a V-to-V vector (V-to-V hypothesis). It has also been suggested that proprioception could be ignored in normal subjects when vision is available (Bock and Eckmiller 1986). According to this hypothesis, the simplest movement vector would be V-to-V.

The third possible hypothesis is that hand position encoding results from a fusion of visual and proprioceptive information. Accordingly, the movement vector would be VP-to-V (cf. Fig. 1). This hypothesis would fit with the finding that viewing the hand before movement has a major effect on pointing variability (Desmurget et al. 1995; Rossetti et al. 1994c). By contrast, a hypothesis based on a V-to-V vector predicts a major effect on constant error, and a hypothesis based on a P-to-V vector predicts no effect on constant error.

To test between these three possible elementary mechanisms (V-to-V, P-to-V, and VP-to-V), an experiment was designed in which visual and proprioceptive information about initial hand position was dissociated by means of prisms without altering the view of the target. If the movement vector was to be encoded on a V-to-V basis, then dissociating the seen hand and the felt hand should result in a pointing bias equal to the amount of visual shift. Conversely, if no effect of the dissociation was observed, it should be concluded that vision is not used to encode hand position. Alternatively, if movement vector encoding resulted from a fusion between discordant visual and proprioceptive information (VP-to-V vector), then the pointing bias should be lower than the prismatic shift (cf. Fig. 1).

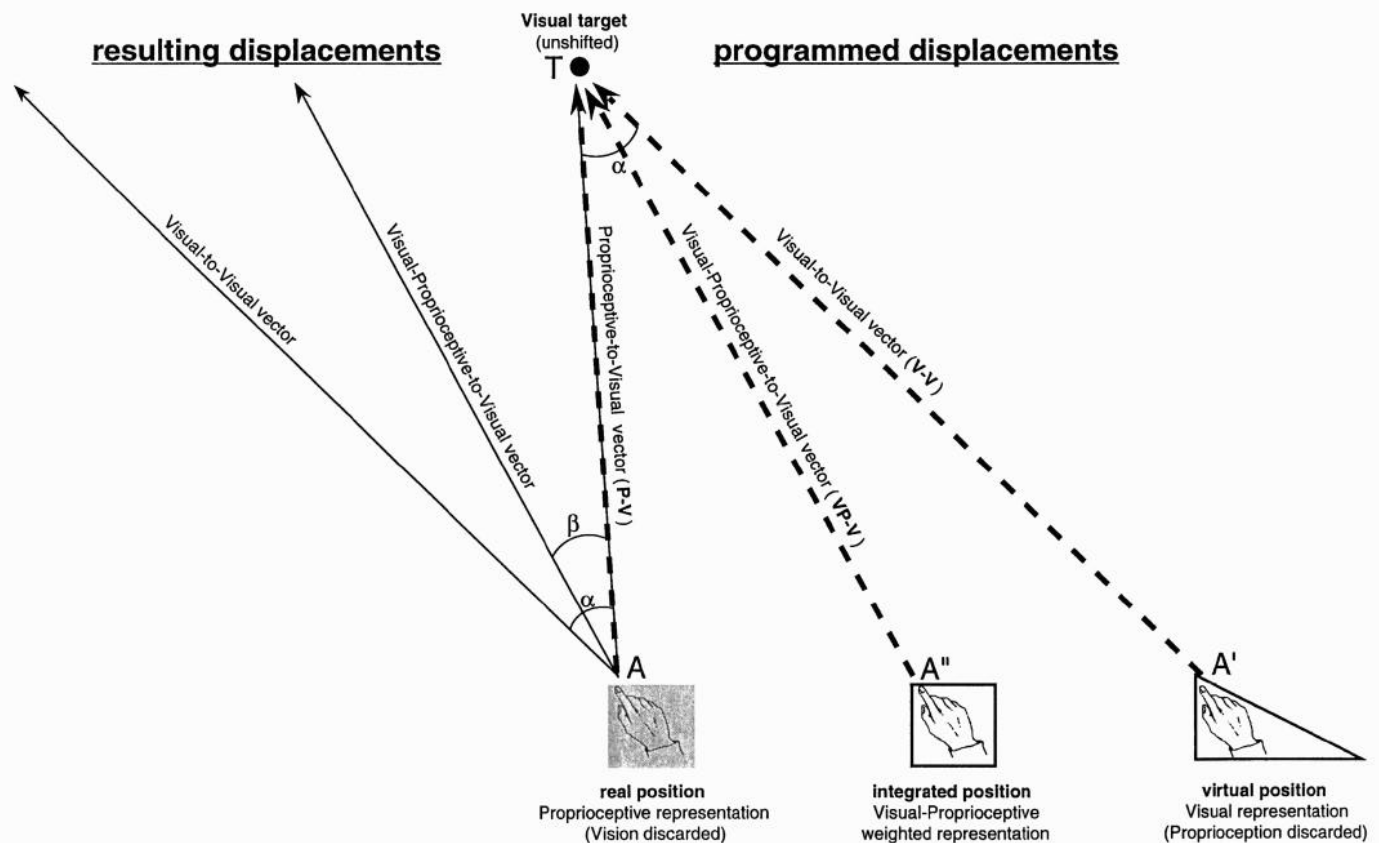


FIG. 1. Hypotheses about vectorial movement coding for visually directed pointing. The possible sensory representations of movement are displayed together with the corresponding predictions of resulting movement in space. For the sake of simplicity, trajectories are presented as straight lines and the horizontal axis has been extended. According to the visual-to-visual (V-to-V) hypothesis, the movement vector would be encoded from the visual information about hand position (when available) and would discard the proprioceptive information. The corresponding deviation angle  $\alpha$  should be equal to  $\arctg(AA'/AT)$ . According to the proprioceptive-to-visual (P-to-V) hypothesis, the movement vector would be encoded from the proprioceptive information about hand position and would discard the visual information. According to a 3rd hypothesis [visual-proprioceptive-to-visual (VP-to-V) hypothesis], the movement vector would be encoded starting from an intermediate position resulting from a weighted fusion of the 2 sources of sensory information. This weighted position is represented here for an equal contribution of vision and proprioception. The corresponding deviation angle  $\beta$  should be equal to  $\arctg(AA''/AT)$ .

In addition, one cannot reject a compound hypothesis a priori. Movements could be programmed as a V-to-V vector and then be subjected to an on-line feedback comparing felt hand position to visual target location (P-to-V). This visual-to-kinesthetic feedback loop has been suggested by previous studies (Prablanc and Martin 1992; Prablanc et al. 1986). To evaluate this hypothesis, both terminal error and initial movement direction need to be computed.

Parts of these results have been presented at the Laval symposium on deafferentation and the role of sensory afferent in human motor control (Rossetti et al. 1993a) and are part of an unpublished PhD dissertation (Rossetti 1993).

## METHODS

### Subjects

Six healthy subjects (3 females and 3 males, aged from 26 to 35 yr) volunteered in this experiment. All of them reported a normal visual acuity. They were naive about the purpose of the experiment and uninformed about the presence of visual manipulation by prisms.

### Device

The experimental device was similar to that described in Rossetti et al. (1994c). It consisted of a horizontal table on which visual targets were presented. Subjects had to point at each target without vision of the moving limb. Subjects were seated on a dentist's chair and were instructed to point at their own pace with the preferred hand, using their best speed-accuracy tradeoff. They were free to move the head, so that no additional pointing errors would arise from position signals related to nonoptimal head posture (cf. Rossetti et al. 1994b). To minimize the variability of starting position across trials, a tactile mark was placed on the table, near the chest, for use by subjects to position the finger in the dark between trials. Care was taken to ensure that the arm was in a comfortable posture when resting at the starting point, and subjects were instructed to use the same initial posture between sessions in order to avoid possible biases in the encoding of initial finger position (Rossetti et al. 1994a). An array of light-emitting diodes (LEDs) was suspended over the subject's head and a half-reflecting mirror ( $380 \times 180$  mm) was placed between the eyes and the table, so that the virtual image of the LEDs projected onto the table surface. Four targets were used, located at 10, 20, 30, and 40° on the right side of sagittal axis of the body, 575 mm in front of the subject's vertical axis.



### Experimental conditions

A visual cue for finger position before movement was provided by a yellow LED (5 mm diam) attached to the tip of the right index finger [it has been shown elsewhere that viewing only the fingertip has a similar effect on pointing variability to viewing the whole hand (Rossetti 1993)]. Targets were lit for 2 s. For each session, each target was presented 10 times in a random order.

In the displaced fingertip (DT) condition, the view of the fingertip was displaced by prisms. Fresnel lenses (15 diopters) were placed on the mirror in such a way that the hand at its starting point (20 cm in front of the vertical body axis and 40 cm below the eyes) was virtually displaced toward the right by  $8.55^\circ$  (thus corresponding to an absolute shift of 41 mm, shown as A-A' in Fig. 1.). This displacement produced a rotation of the hand-to-target visual vector by  $\arctg(AT/AA')$ , i.e.,  $6.2^\circ$ . This particular value was chosen because preliminary experiment had shown that stronger lenses (20 or 25 diopters) were detected by the subjects and elicited conscious cognitive strategies. In the view of fingertip (VT) condition, two superimposed fresnel lenses were used (left to right) such that the optical axis was not displaced. This condition was used as a control for the DT condition. In both conditions the target was seen through the mirror without displacement. In contrast with classical prism adaptation experiments (e.g., Bedford 1989; Jakobson and Goodale 1989; Redding and Wallace 1992; Rossetti et al. 1993b), no error feedback was provided in order to prevent adaptation to the visual shift. In addition, to prevent the static long-term adaptation of registered gaze position under prolonged exposure to displaced vision (Craske 1967), in both conditions the finger LED was lit only for 300 ms before target presentation until movement onset. Subjects performed two blocked sessions (VT and DT conditions) in random order.

### Movement analysis

**CONSTANT ERRORS.** Because the visual shift consisted of a 41-mm horizontal translation of the viewed fingertip along the X-axis, constant errors were measured along the X- and Y-axes rather than in a polar system of coordinates such as direction-amplitude. X-errors were measured frontal to the subject as the mean difference between movement endpoint and target position. Errors were also measured along the Y axis (Y-errors).

**VARIABLE ERROR.** Variable error was computed from the 10 repetitions per target and per condition by the same subject (variable error =  $\pi \cdot SD_x \cdot SD_y$ ,  $SD_x$  and  $SD_y$  being the standard deviations of the pointing errors measured along the X-axis and the Y-axis, respectively).

**TEMPORAL PARAMETERS.** Reaction time (RT) and movement time (MT) were measured to check for possible speed-accuracy biases between the two experimental conditions.

**INITIAL MOVEMENT DIRECTION.** To check whether the whole movement was affected in the same way or whether it was subjected to in-flight corrections from an initial V-to-V direction to a final P-to-V direction (thus resulting in a terminal VP-to-V-like error), initial movement direction was measured in the DT and VT conditions. Initial movement direction was computed on the successive fingertip positions sampled from movement onset to movement onset + 80 ms (i.e., 17 frames). The slope of the linear regression fitting these points provided an estimate of initial movement direction.

### Statistical analysis

Means and standard deviations presented in RESULTS were calculated from the 6 subjects  $\times$  4 targets = 24 values. Differences between the two experimental conditions, and between experi-

mental results and theoretical expectations, were tested by a paired Student's *t*-test (24 pairs of values). Analysis of variance (ANOVA) and Scheffé's post hoc tests were used to check for target and rank effects.

## RESULTS

### Constant errors

As expected (because the prisms did not introduce any bias along the Y-axis), constant errors measured orthogonal to the prismatic shift (Y-errors) did not vary significantly across the two experimental conditions (37 mm in the VT condition and 39 mm in the DT condition, paired  $t(23) = 0.37$ , not significant). The absence of prism effect on the Y-error shows that the prism effect is specific to the alteration produced. Moreover, no target eccentricity effect was observed in these two conditions [ $F(3,23) < 0.06$ , not significant].

X-errors were 22 mm in the DT condition and 35 mm in the VT condition (Fig. 2). No significant target eccentricity effect was observed in each of the two conditions [ $F(3,23) < 1.7$ , not significant]. To check for a possible prism adaptation in the blocked DT session, an ANOVA was computed to compare errors trial by trial. No significant rank effect was observed in the DT condition, and in particular no significant difference between the first and the last trial in the sequence [ $F(9,239) = 0.56$ ,  $P > 0.80$ ].

X-errors obtained in the DT and VT conditions were compared. This analysis will be used to test the P-to-V hypothesis. Visually shifting the fingertip to the right (DT condition) induced a small pointing bias to the left with respect to pointings observed under the VT condition. The X-error measured in the DT condition was significantly shifted toward the left [mean difference = 13 mm, paired  $t(23) = -5.78$ ,  $P < 0.0001$ ]. Because the P-to-V hypothesis predicted no effect of the prisms on pointing accuracy, it cannot account for these data. Again, no effect of target eccentricity was observed on the difference between the VT and DT conditions [ $F(3,23) = 0.22$ , not significant].

After the DT session, subjects were asked to report their perceptions of the experimental condition. Only one of the six subjects detected the optical shift of the fingertip. Nevertheless, this subject was ranked third when considering the magnitude of the prismatic effect.

The endpoint bias observed in the DT condition corresponded to about one third (13 mm, 31.7%) of the effect predicted by the V-to-V hypothesis (41 mm) (Fig. 2). The constant X-error obtained in the DT condition was thus compared with the value expected on the basis of the V-to-V vector hypothesis (i.e., the X-error value obtained in the VT condition minus the 41 mm of virtual shift). The difference between the experimental results and the V-to-V prediction was clear-cut [paired  $t(23) = 12.34$ ,  $P < 0.0001$ ] (see Fig. 2). The process of locating the hand before movement therefore cannot rely on vision only.

### Variable error

When the view of the fingertip LED was displaced through prisms, variable error was significantly increased from 425 to 565 mm<sup>2</sup> [paired  $t(23) = 2.11$ ,  $P < 0.05$ ]. No target

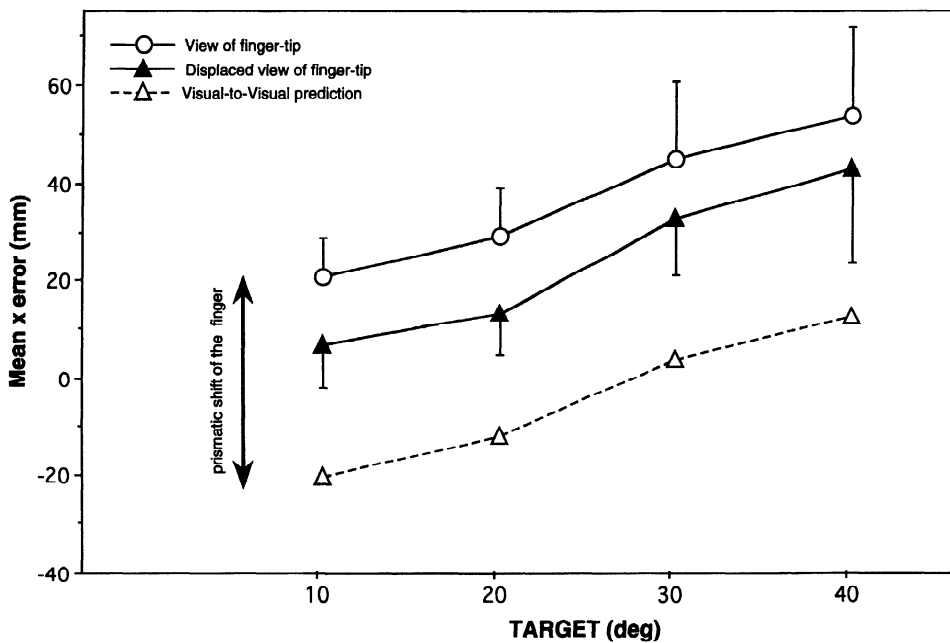


FIG. 2. X-errors obtained in the 2 experimental conditions and predicted by the V-to-V vector hypothesis. In the view of fingertip (VT) condition, a tendency to point to the right of the target was observed ( $\circ$ ). As predicted by the V-to-V vector hypothesis, the pointing should have been shifted toward the left by  $\sim 41$  mm when the hand was shifted toward the right by 41 mm ( $\Delta$ ). By contrast, experimental results obtained in the displaced fingertip (DT) condition showed that pointings were displaced by  $\sim 13$  mm. Although errors observed in the DT condition were significantly different from those obtained in the VT condition, the main difference was observed between the DT condition and the V-to-V vector predictions. This results could be explained by an unbalanced weighting of the visual (31%) and the proprioceptive (69%) information used to encode hand position before movement.

effect was observed in the two experimental conditions [ $F(23,3) < 1.2$ ,  $P > 0.35$ ].

#### Temporal parameters

Movement temporal parameters were also tested. RT was significantly longer in the DT condition ( $532 \pm 277$  ms, mean  $\pm$  SD) than in the VT condition ( $452 \pm 192$  ms, mean  $\pm$  SD) [paired  $t(23) = 2.62$ ,  $P < 0.02$ ]. A slight (42 ms) lengthening of MT was also noticed in the DT condition ( $594 \pm 123$  ms, mean  $\pm$  SD) compared with the VT condition ( $552 \pm 124$  ms, mean  $\pm$  SD) [paired  $t(23) = 4.22$ ,  $P < 0.0005$ ].

#### Initial movement direction

The mean angular displacement of initial movement direction observed in the DT condition relative to the VT condition was  $0.9^\circ$ . Figure 3 shows that a consistent difference in initial movement direction was observed between the VT and DT conditions for every target location [paired  $t(23) = 1.90$ ,  $P < 0.04$ ]. The difference in initial movement direction between the DT and VT conditions was then compared with the theoretical value predicted by the V-to-V hypothesis (i.e., 41 mm projected at  $375$  mm =  $6.24^\circ$ ). The predicted and the observed values differed significantly [paired  $t(23) = 15.2$ ,  $P < 0.0001$ ], which allowed to reject the initial V-to-V hypothesis.

#### DISCUSSION

The main result of the present experiment is that displacement of the visual information about hand position before movement induced a pointing bias in the direction opposite to the visual shift. Although this work was not aimed at testing the vectorial coding of movement hypothesis, the present result strongly supports the VP-to-V hypothesis.

The constant error obtained in the VT condition was very

close to that obtained in full darkness with the same experimental device (Desmurget et al. 1995, *experiment 1*), and comparable with that obtained in a similar experiment performed using another device (Rossetti 1994a). Significant constant errors are always observed when movements are performed without visual feedback (referred to as visual open-loop condition) (e.g., Prablanc et al. 1979). Several hypotheses can account for these errors. They are possibly related to geometric or biomechanical factors, which are only partially compensated by proprioceptive feedback in normal subjects (Gordon et al. 1995). Alternatively, they can be interpreted as linear approximations in sensorimotor transformations, as suggested by Socchting and Flanders (1989) in a pointing experiment performed in a three-dimensional space, where they reported constant errors of up to 15 cm. Thus constant errors observed in our control VT condition may correspond to a baseline level for the visual open-loop condition. Constant error obtained in the DT condition is interpreted relative to that baseline. The visual shift of initial hand position induced a nearly constant pointing bias in the direction opposite to the visual shift. Conversely, shifting the hand in the opposite direction should produce opposite shifts in hand pointing. Thus the relative decrease in constant error observed in the DT condition cannot be considered as a clue for an absolute improvement in accuracy. This interpretation is further supported by the lack of significant difference in Y-errors between the VT and DT conditions. If the conflict between visual and proprioceptive information led the subject to rely more on proprioception (which may produce more accurate movement), then one would expect both X- and Y-errors to decrease in the DT condition compared with the VT condition.

The pointing bias observed in the DT condition was equal to only about one third of the virtual hand displacement and was constant across target eccentricities (Fig. 2). This result fits with the VP-to-V coding hypothesis, suggesting that the initial hand position code resulted from a fusion of visual

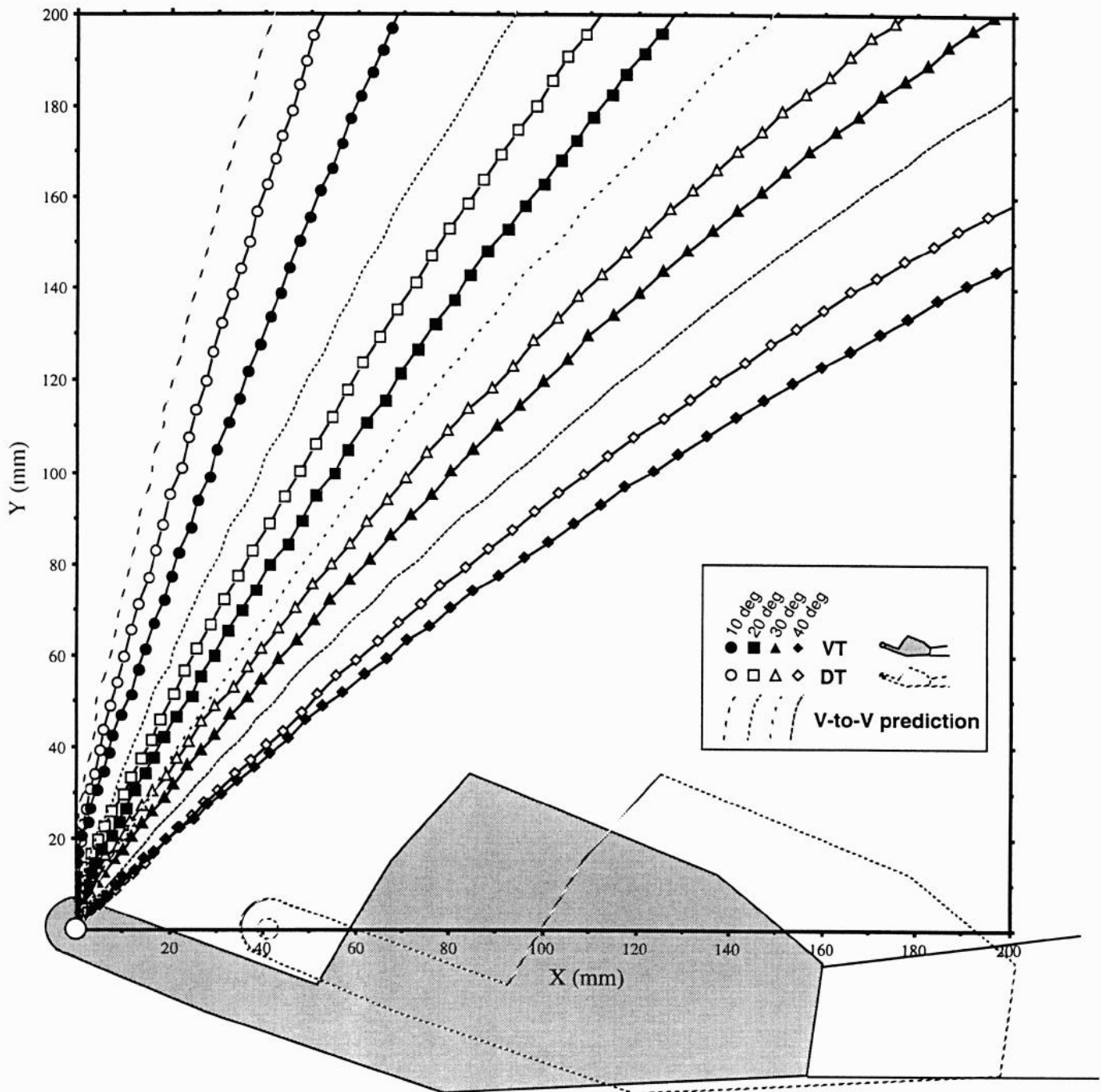


FIG. 3. Initial movement directions observed in the VT and DT conditions and predicted by the V-to-V hypothesis. Mean fingertip positions sampled during pointings to the 10, 20, 30, and 40° targets in the VT condition (filled symbols) and the DT condition (open symbols) (individual *subject PD*). Trajectories predicted by the V-to-V hypothesis (broken lines) have been obtained by rotating trajectories observed in the VT condition so as to reproduce the theoretical 41-mm shift in endpoint (i.e., 6.2° counterclockwise rotation). Hand position viewed through the prisms (outline) is shifted 41 mm to the *right* from actual initial hand position (shaded area). Please note that DT trajectories tend to diverge from VT trajectories early in the movement, but also diverge from trajectories predicted by the V-to-V hypothesis.

and proprioceptive information, which affected the whole movement. However, the slight lengthening of MT observed in the DT condition relative to the VT condition suggests that in-flight movement corrections may have occurred. If this was the case, then the observed pointing bias might result from two sequential processes: a first process driving the hand from its starting position along the V-to-V vector,

and a second process applying a correction based on a P-to-V dynamic motor error. Accordingly, a V-to-V vector would be used to compute the initial movement direction. This hypothesis was, however, rejected by the movement analysis, which showed that initial movement direction was different from that predicted by the V-to-V hypothesis. Moreover, the difference in initial movement direction mea-



sured between the DT and VT conditions was not significantly different from the difference in terminal accuracy, which suggests that in-flight movement corrections, if any, were of little extent. It may be proposed that late feedback computation has been affected by information provided before movement (as shown in Desmurget et al. 1995; Rossetti et al. 1994a) in the same way as was the initial movement direction. Indeed, if the hand position code provided by proprioception is reinterpreted after the hand was seen, then both feedforward and feedback control based on proprioceptive information should be biased.

The results obtained on both terminal error and initial movement direction demonstrate that altering the sight of initial hand position by a given amount does not alter pointing by an equal amount. Consequently, the pointing trajectory obtained when the view of the static hand is shifted is not identical to the trajectory predicted by the V-to-V hypothesis (this theoretical trajectory should be encoded from the viewed hand position to the viewed target position) (see Fig. 3). This result has strong implications within the framework of the vectorial coding hypothesis. It shows that the hand position signal implemented in the motor program is derived from both visual and proprioceptive information. Should a hypothetical movement vector be processed by the sensory-motor system, the strict V-to-V encoding mechanism can be discarded. It has been already shown that vision can assist proprioception in encoding initial hand position (Elliott et al. 1991; Prablanc et al. 1979; Rossetti et al. 1994c). Our present result supports this latter idea, and further suggests that the initial hand position signal is derived from a fusion of the two heterogeneous types of sensory information.

The present results appear to be contradictory with the classical notion of visual capture, where a strong visual dominance over proprioception is usually reported (e.g., Pick et al. 1969; Rock 1966; Welch 1986). Interestingly, a number of attempts have been made to reduce this dominance, without success (e.g., Warren 1979). Our finding indicates that proprioceptive information may have a higher weight when the localization process is concerned with body parts involved in the action.

Variable error was larger in the DT condition than in the VT condition. This result is unlikely to be related to a speed-accuracy tradeoff, because movements were slower in the DT condition than in the VT condition. Interestingly, the variable error value obtained in the DT condition was very close to that obtained in full darkness with the same experimental device (Desmurget et al. 1995, *experiment 1*). This comparison suggests that the decrease in pointing variability observed when the hand is briefly viewed before the movement as compared with full darkness (Desmurget et al. 1995; Elliott et al. 1991; Prablanc et al. 1979; Rossetti et al. 1994c) is contingent on a spatial realignment or cross-recalibration between vision and proprioception. When the information from both sources is congruent, the resulting hand position is more sharply represented and subsequent pointing variability is reduced (Desmurget et al. 1995; Rossetti et al. 1994c). Neurophysiological studies support the notion of enhanced sensory representation under coherent stimuli in the nervous system. For example, in the cat, superior colliculus neurons that normally fire for visual and for auditory

stimuli increase their discharge by a multiplicative rather than an additive factor when congruent auditory and visual stimuli are provided (Meredith and Stein 1986). In this vein it can be suggested that multisensory integration cannot achieve a sharper representation when proprioceptive and visual signals are misaligned in space. This would account for our observation that pointing variability in the DT condition was very similar to that reported in a full darkness condition (Desmurget et al. 1995).

The increase in RT observed in the DT condition suggests that the discrepancy between visual and proprioceptive information induced a modification in motor preparation. An increase in RT has already been reported by Jackson and Zangwill (1952) in another condition of visual-proprioceptive discrepancy. In their experiment, subjects were asked to flex a finger according to verbal instructions under various visual feedback conditions. RT was longer when the hand was viewed in a mirror than under normal vision. A temporal reorganization in eye-hand coordination has been also reported during the very first trials of wedge prism exposure, i.e., before the visual-proprioceptive discrepancy was resolved through adaptation (Rossetti et al. 1993b).

Although our subjects were unaware of the hand visual shift, the lengthening of reaction time observed here in DT relative to VT suggests that the discrepancy between visual and proprioceptive information may have altered normal motor preparation. If information arising from different sensory systems is bound together to produce a motor output, the triggering of movement onset may be achieved earlier during movement preparation when visual and proprioceptive information is aligned in space. Indeed, no significant increase of hand RT was found during prism exposure when the initial hand position was lying out of the visual field (Rossetti et al. 1993b).

The pointing bias observed here, when visually shifting hand position by prisms without shifting the target, strongly confirms that visual information about hand position before movement contributes to motor programming (Jeannerod 1988; Jeannerod and Prablanc 1983) and can affect both systematic and variable errors. The difference in constant error observed between the VT and DT conditions also demonstrates that the putative movement vector is not merely encoded on a simple P-to-V basis, but rather that encoding the vector's origin involves a fusion of visual and proprioceptive information. Even though no specific instruction was orienting the subject's attention toward the viewed fingertip, it is remarkable that this visual information did bias the pointings.

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