

Michel Desmurget · Philippe Vindras · Hélène Gréa  
Paolo Viviani · Scott T. Grafton

## Proprioception does not quickly drift during visual occlusion

Received: 20 March 1999 / Accepted: 8 May 2000 / Published online: 25 July 2000  
© Springer-Verlag 2000

**Abstract** Several perceptual studies have shown that the ability to estimate the location of the arm degrades quickly during visual occlusion. To account for this effect, it has been suggested that proprioception drifts when not continuously calibrated by vision. In the present study, we re-evaluated this hypothesis by isolating the proprioceptive component of position sense (i.e., the subjects were forced to rely exclusively on proprioception to locate their hand, which was not the case in earlier studies). Three experiments were conducted. In experiment 1, subjects were required to estimate the location of their unseen right hand, at rest, using a visual spot controlled by the left hand through a joystick. Results showed that the mean accuracy was identical whether the localization task was performed immediately after the positioning of the hand or after a 10-s delay. In experiments 2 and 3, subjects were required to point, without vision of their limb, to visual targets. These two experiments relied on the demonstration that biases in the perception of the initial hand location induced systematic variations of the movement characteristics (initial direction, final accuracy, end-point variability). For these motor tasks, the subjects did not pay attention to the initial hand location, which removed the possible occurrence of confounding cognitive strategies. Results indicated that movement characteristics were, on average, not affected when a 15-s or 20-s delay was introduced between the positioning of the arm at the starting point and the presentation of the target. When considered together, our re-

sults suggest that proprioception does not quickly drift in the absence of visual information. The potential origin of the discrepancy between our results and earlier studies is discussed.

**Key words** Proprioception · Vision · Reaching · Pointing · Position sense

### Introduction

As early as 1880, Bowditch and Southard reported that the ability to determine the position of the hand in space tends to degrade quickly during visual occlusion. The validity of this pioneering observation was confirmed in a large number of subsequent studies (Block 1890; Paillard and Brouchon 1968; Craske and Crawshaw 1975; Velay 1984; Wann and Ibrahim 1992), leading most researchers to admit that proprioception drifts when it is not continuously calibrated by vision. With respect to this relative consensus, however, two points are worth noting. First, a number of experiments failed to reveal a progressive degradation of the ability to estimate the hand location when vision was occluded (DelRey and Lichter 1971; Horch et al. 1975; Lee and Kelso 1979). Second, the interpretation of the main studies supporting the concept of “proprioceptive drift” is generally not as straightforward as asserted. As an illustration of this point, consider the experiment carried out by Paillard and Brouchon (1968). The apparatus allowed the subjects to move their hands along two parallel vertical tracks. At the beginning of each trial, the left hand was moved actively or passively to a predetermined position. The subject was then instructed to match the left-hand vertical position with the right hand, either immediately or after a delay. A problem with this procedure is that not only the static proprioceptive signal was available at zero delay, but also the information related to the magnitude of the performed displacement. This additional cue, which vanishes progressively over time, may have been used to enhance the positioning of the right hand at zero

---

M. Desmurget · S.T. Grafton  
Department of Neurology,  
Emory University School of Medicine,  
Atlanta, GA 30322, USA

M. Desmurget · P. Vindras · P. Viviani  
Faculté de Psychologie et des Sciences de l'Éducation,  
Université de Genève, 1227 Carouge, Switzerland

M. Desmurget · H. Gréa  
Espace et action, Institut National de la Santé  
et de la Recherche Médicale Unité 534,  
16 avenue du Doyen Lépine, Case 13,  
69676 Bron Cedex, France

delay. Arguments supporting this hypothesis are provided by psychophysical experiments demonstrating the existence of strong interference effects between hand-location and movement-magnitude information in short-term memory (Walsh et al. 1979; Imanaka and Abernethy 1992). The uncertainty attached to the interpretation of the Paillard and Brouchon experiment was also present in the widely quoted study carried out by Wann and Ibrahim (1992). In this study, the target hand rested, in view, on a table. Suddenly, the light was turned off, and the subject was required to estimate the location of his index fingertip by pointing with the contralateral hand. With respect to this procedure, one may not exclude the hypothesis that the accuracy degradation observed when a delay was introduced between the right-arm positioning and the left-arm pointing was not related to a proprioceptive drift, but to the progressive deterioration of the visual trace. In particular, one may hypothesize that external landmarks were used to locate the hand in the immediate-pointing condition, but not in the delay-pointing condition. Evidence supporting this view were provided by Elliott and Madalena (1987; Elliott 1988), who showed that the visual information related to the movement environment degrades quickly after visual occlusion. Even if this possibility is rejected, the interpretation of the Wann and Ibrahim (1992) experiment still remains ambiguous. Indeed, it lies on the a priori hypothesis that proprioception drifts and that vision recalibrates the proprioceptive signal (Jeannerod 1988). This view agrees with the classical notion of visual capture, according to which vision "attracts" proprioception when these two senses are misaligned with respect to each other (Rock 1966; Welch et al. 1979; Mon-William et al. 1997). However, recent psychophysical experiments suggest that vision might influence the ability to locate the hand at rest, not by realigning the proprioceptive space with respect to the visual space, but by generating a visual-proprioceptive multimodal representation that is more accurate than each of the unimodal representations alone (Desmurget et al. 1995; Rossetti et al. 1995; van Beers et al. 1996). If such is the case, an alternative explanation to the Wann and Ibrahim study (1992) would be that the representation of the hand location progressively shifted from a multimodal representation to a less-accurate unimodal representation involving the proprioceptive signal alone.

It is worth noting that all the studies evoked in the previous paragraph were conducted at a perceptual level. That is, the subjects were explicitly required to indicate the location of their fingertip or to match the posture of one of their limbs with the other limb. Due to this fact, one may not rule out the hypothesis that part of the contrasting observations reported in the literature reflect the various contribution of memorial, attentional, or strategic factors (Horch et al. 1975; Wann and Ibrahim 1992). In light of this remark, it appears worth testing the existence of a proprioceptive drift in a pointing task for which the subjects do not pay attention to the initial hand location. If proprioception drifts, movement accuracy

should degrade when the subjects have to wait in the dark before pointing. Indeed, it has been demonstrated that pointing errors reflect, in part, biases in the estimation of the initial hand location (Prablanc et al. 1979; Bock and Eckmiller 1986; Jaric et al. 1992; Bock and Arnold 1993; Rossetti et al. 1994, 1995; Desmurget et al. 1995, 1997b; Ghilardi et al. 1995; Vindras et al. 1998; for a review, see Desmurget et al. 1998). With respect to this idea, however, it should be stressed that the coordinate system and neural mechanisms used to either consciously locate the hand during perceptual tasks or unconsciously locate the hand prior to visually directed movements may be different (Bridgeman et al. 1981; for a review, see Rossetti 1998; Goodale and Haffenden 1998). This leaves open the possibility that proprioception drifts during perceptual tasks such as matching the right hand posture with the left hand, but not during motor tasks such as reaching to a visual target in the dark.

In summary, the present study addresses two main questions. First, does accuracy really degrade over time when a subject attempts to estimate the location of his hand in space on the basis of proprioceptive information. Second, does a degradation occur in the context of a motor tasks requiring to point to a visual target.

---

## Experiment 1

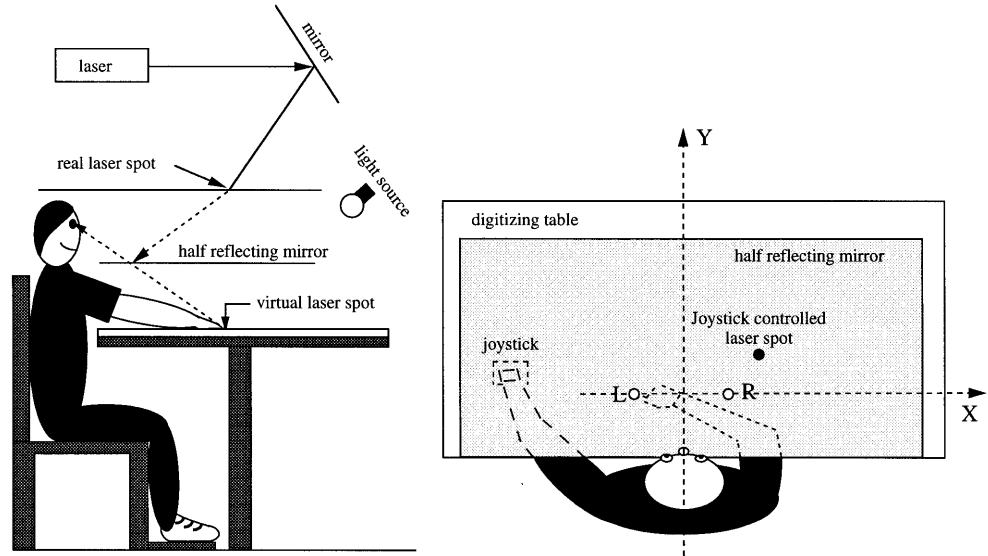
In this first experiment, we examined the issue of whether the ability to estimate the location of the arm degrades quickly during visual occlusion when the subject relies exclusively on proprioception to perform the task. A perceptual study was carried out in which the subjects were required to evaluate the position of their right hand. Three main precautions were adopted to avoid experimental artifacts: (1) the target hand was guided (by the experimenter) to its resting point through a non-straight random displacement; (2) vision was turned off a few centimeters before the hand resting location was reached; and (3) the estimation of the target hand location did not involve a pointing movement performed with the contralateral arm, but consisted of positioning a joystick-controlled visual spot.

### Materials and methods

#### *Apparatus and procedure*

Ten right-handed subjects, aged from 21 to 43 years, participated in the experiment. They had normal visual acuity and were naive about the purpose of the study. A schematic representation of the experimental apparatus is provided in Fig. 1. Each subject was seated comfortably in front of a digitizing table (Numonics Corporation, Montgomeryville, Penn., USA; model 2200–2436; nominal accuracy: 0.025 mm, temporal resolution: 200 Hz). A laser spot (4 mm in diameter) could be projected on the table through a half-reflecting mirror. The spot position was controlled by a set of galvanometric mirrors, which were driven by the subject through a joystick placed on their left side. Two resting positions were defined. One (L) was 12 cm to the left of a central point located 26 cm in front of the subject's sternum. The other (R) was placed symmetrically to L with respect to the central point. A position-recording stylus was held by the subject with the right hand as close as possible to its tip. This allowed control of a possible change in the hand resting position during visual occlusion. The experimenter (but not the subject) could see the resting locations (L, R) and the instantaneous stylus position on the screen of the controlling computer.

**Fig. 1** Schematic representation of the experimental apparatus used in experiment 1. For explanation of abbreviations etc., see text



Each trial involved 6 steps:

1. The light was turned on to update representation of the hand location.
2. The experimenter guided the subject's right hand toward one of the two resting positions using the information displayed on the computer screen. This positioning movement was, however, not totally passive inasmuch as the subject had to provide the motor energy necessary to move the guided arm. The light remained on until the tip of the stylus was within 4 cm of the required position. This early extinction prevented the subject from visually estimating the initial position of their hand.
3. The laser spot was turned on, either immediately or after a 10-s delay, instructing the subject to use the joystick (with the left hand) to bring the laser spot in coincidence with the (unseen) tip of the stylus. Correct positioning had to be validated 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 target hand.
4. After the required action was completed the spot was turned off.
5. The experimenter moved the subject's hand about 30 cm away from its current location. This step was included to prevent the subject from visually comparing the actual hand position with the position where he/she thought the hand was.
6. The light was turned on again.

In one single session, each subject performed 48 trials (two resting positions  $\times$  two delays  $\times$  12 repetitions). During the session, the two resting positions and the two delays were randomly intermixed.

#### Data analysis

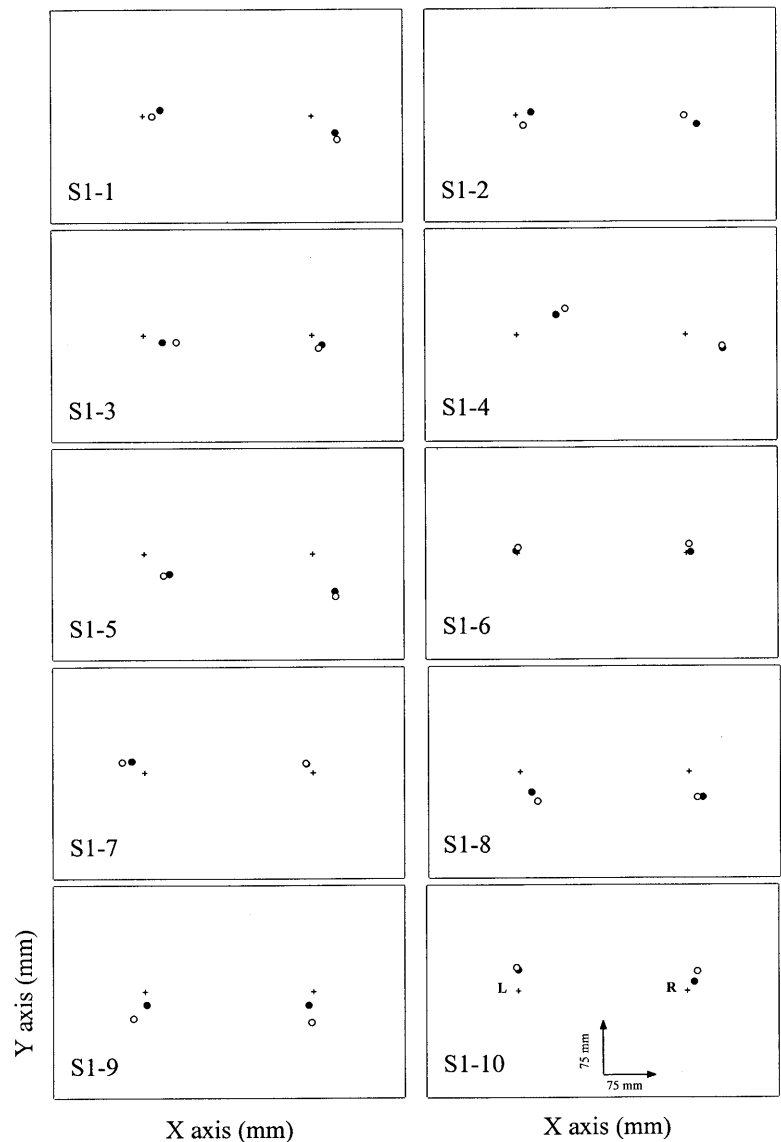
Two error parameters were measured:

1. The systematic error. An orthogonal frame of reference was defined, with the y axis being sagittal and oriented forward, and the x axis being fronto-parallel and oriented rightward (Fig. 1). The systematic error was defined as the vector joining the actual hand position (resting point) to the position indicated by the subject. The components of this vector were  $SE_x$  and  $SE_y$ .
2. The variable error. It was defined as the surface of the 95% confidence ellipsoid of the end-point distribution (the lengths of the axes of this ellipsoid were the eigenvalues of the variance-covariance matrix of the end-point distribution, scaled to contain 95% of the theoretical end-point population; see Johnson and Wichern 1982).

In order to test the influence of the experimental factors on the variable error, a univariate between-subject ANOVA with repeated measures was performed. For the systematic error, which is defined by two parameters ( $SE_x$ ,  $SE_y$ ), a multivariate between-subject ANOVA with repeated measures was used. In this case, the  $F$  value was determined from the Wilk's lambda, using the Rao's approximation (Maxwell and Delaney 1990). The repeated-measures factors were: "resting point" (two levels: L, R), and "delay" (two levels: 0 s, 10 s). Threshold for statistical significance was set at 0.05. For the systematic errors, additional intra-individual analyses were performed, considering that consistent inter-individual variations in the characteristics of the proprioceptive drift may result in non-significant "between-subjects" analyses, even if a drift exists at the individual level (i.e., variations may "cancel" each other in a between-subjects comparison). For the within-subject analyses ( $n=10$ ), two-way MANOVAs were performed with "resting point" and "delay" as experimental factors. Note that within-subject analyses could not be computed for the variable error inasmuch as there is only, by definition, one variable error per subject and per condition. This should, however, not affect the results considering that the variable error is expected to increase, for all subjects, if the proprioceptive signal degrades over time.

To test whether within-subject analyses globally confirmed or rejected the  $H_0$  hypothesis, we performed both a three-way MANOVA (subject  $\times$  delay  $\times$  resting point) and a Kolmogorov-Smirnov test. We computed the MANOVA because it is a standard extension of the individual MANOVAs carried out for each subject. However, this analysis may have a limited power and its statistical validity is questionable. Indeed, the factor "subject" represents a random factor, which should be investigated with a model II or model III of variance analysis, rather than with the model I akin to the MANOVA. The Kolmogorov-Smirnov test allows this difficulty to be circumvented. This powerful test (Siegel 1956) is a test of goodness of fit between the distribution of a set of sample values and some specified theoretical distribution. Within the context of the present experiment, it allows the determination of whether the  $F$  values of the delay factor in the ten individual MANOVAs are distributed as a  $F(2,43)$ . Because subject is a random variable, the computed  $F$ -test is also a random variable which must be distributed according to a  $F(2,43)$  statistic if localizations are independent of the delay.

**Fig. 2** Mean hand-location estimation for all subjects (S1-1 to S1-10) and the two resting positions (*cross*), under the delay (*white circles*) and no-delay (*black circles*) conditions (experiment 1)



## Results

### General observations

The mean time elapsed between the beginning of the trial (light-on) and the extinction of the light (hand within 4 cm from the resting location) was equal to 1.7 s (no-delay:  $1.7 \pm 0.2$  s; delay:  $1.7 \pm 0.3$  s). The time elapsed between the extinction of the light and the actual positioning of the hand at rest was equal to 1.9 s (no-delay:  $1.9 \pm 0.5$  s; delay:  $1.8 \pm 0.4$  s). Validation of the hand positioning by the experimenter (visual spot on) took, on average, 2.8 s (no-delay:  $2.8 \pm 0.4$  s; delay:  $2.9 \pm 0.2$  s). The subjects needed, on average, 5 s to bring the laser spot in coincidence with their unseen hand (no-delay:  $4.8 \pm 0.8$  s; delay:  $5.2 \pm 1.0$  s).

The previous observations indicate that the two delays compared in this experiment were either 7.6 s ( $2.8 + 4.8$ ) and 18.1 s ( $2.9 + 5.2 + 10$ ) if one assumes that dynamic proprioception does not drift (i.e., total time elapsed between the positioning of the target hand at rest and the validation of the trial) (Wann and Ibrahim 1992) or 9.5 s ( $1.9 + 2.8 + 4.8$ ) and 19.9 s ( $1.8 + 2.9 + 5.2 + 10$ ) if one assumes that proprioception may drift even when the arm is moving (i.e., total time elapsed between the extinction of the light and the validation of the trial). For the sake of simplicity, we will still use the labels “no-delay” and “delay” in the following, despite the

existence of a delay between the extinction of the light and the actual validation of the trial by the subject. The potential influence of the delay required to position the hand and manipulate the laser spot will be considered in the discussion.

### *The estimated hand location did not vary significantly as a function of the resting delay*

All the subjects exhibited consistent systematic errors when required to indicate the position of their unseen hand with a light spot, immediately after the end of the arm positioning. Although the pattern of error varied consistently from subject to subject, the bias in the estimation of the hand location tended to be directed rightward and toward the subjects' body (x coordinate:  $15.5 \pm 22$  mm; y coordinate:  $-8.6 \pm 25$  mm; see Fig. 2). When averaged across the experimental conditions, the mean distance between the actual and estimated resting point was equal to  $32.4 \pm 18.5$  mm. Between-subject analyses did not reveal any significant variation of the systematic errors as a function of either the hand resting location ( $F_{2,8} = 2.7$ ;  $P > 0.10$ ) or the delay factor ( $F_{2,8} = 0.6$ ;  $P > 0.55$ ). This latter observation argues against the hypothesis that the proprioceptive signal drifts over time. We did not observe any significant interaction between the delay factor and the resting location ( $F_{2,8} = 0.7$ ;  $P > 0.50$ ).



**Table 1** Intra-individual MANOVAs involving the systematic errors (experiment 1). Significant effects are represented in *bold characters* ( $P < 0.05$ , uncorrected for multiple comparisons). The  $F$  values were determined from the Wilk's lambda, using the Rao's approximation (Maxwell and Delaney 1990)

Subject	Resting point $F(2,43)$	Delay $F(2,43)$	Resting point $\times$ delay $F(2,43)$
S1	<b>F=13.80 (P&lt;0.0001)</b>	$F=1.37 (P>0.25)$	$F=0.65 (P>0.50)$
S2	$F=1.10 (P>0.30)$	<b>F=3.72 (P&lt;0.04)</b>	$F=3.06 (P>0.05)$
S3	<b>F=11.97 (P&lt;0.0001)</b>	$F=1.19 (P>0.30)$	$F=2.78 (P>0.05)$
S4	<b>F=15.85 (P&lt;0.0001)</b>	$F=0.44 (P>0.60)$	$F=0.39 (P>0.65)$
S5	<b>F=15.68 (P&lt;0.0001)</b>	$F=0.67 (P>0.50)$	$F=0.73 (P>0.45)$
S6	$F=0.8 (P>0.45)$	$F=1.86 (P>0.15)$	$F=0.32 (P>0.70)$
S7	<b>F=5.06 (P&lt;0.02)</b>	$F=1.13 (P>0.30)$	$F=1.01 (P>0.35)$
S8	$F=0.41 (P>0.65)$	$F=0.66 (P>0.50)$	$F=1.42 (P>0.25)$
S9	$F=0.50 (P>0.60)$	<b>F=17.56 (P&lt;0.0001)</b>	<b>F=3.90 (P&lt;0.03)</b>
S10	<b>F=5.02 (P&lt;0.02)</b>	$F=1.63 (P>0.20)$	$F=1.08 (P>0.30)$

Intra-individual analyses were performed to test whether the negative results concerning the mean systematic errors were due to significant, but opposite changes in several subjects. As reported in Table 1, two subjects (S1-2, S1-9) exhibited a significant difference in the estimated location of the hand when a waiting period was imposed between the arm positioning and the localization process. Further analyses indicated that this result did not allow the null hypothesis of unchanged systematic errors to be rejected. The Kolmogorov-Smirnov statistic indicated that the individual  $F$ s were distributed according to a  $F(2,43)$  statistic, in agreement with the hypothesis that localizations are independent of the delay factor ( $P > 0.08$ ). A similar conclusion was obtained from the three-way MANOVAs involving the subject factor ( $P > 0.15$ ). The absence of delay-related bias is illustrated in Fig. 2, which displays, for all subjects, the mean location of the estimated end-point for the 0-s and 10-s delays. Further evidence is provided in Fig. 3, which shows that the two end-point distributions largely overlapped for most subjects.

It is worth mentioning, for the sake of completeness, that the estimated hand location varied significantly as a function of the resting location for six of the ten subjects (Table 1; Fig. 2). This indicated that the bias in the proprioceptive representation of the hand location depended on the arm posture. A significant interaction between the delay factor and the resting location was observed for S1-9 (Table 1).

#### *The variable error did not increase significantly with the resting delay*

The surface of the 95% confidence ellipse characterizing the variable error was found to be slightly higher when a delay was introduced between the arm positioning and the localization process (0 s:  $6121 \pm 3042$  mm<sup>2</sup>; 10 s:  $6394 \pm 4881$  mm<sup>2</sup>). The ANOVA indicated that this difference was far from reaching the statistical threshold ( $F_{1,9}=0.18$ ;  $P > 0.65$ ). In fact, the slight increase of the mean surface depended mainly on subject S1-4, who exhibited dramatically large variable errors (see Fig. 3). Without subject S1-4, a slight non-significant decrease of the variable error would have been observed at 10 s with respect to 0 s ( $5372$  vs.  $5100$  mm<sup>2</sup>;  $P > 0.45$ ). This indicates that the non-significant result reported in this experiment is unlikely to represent a false negative inference (or type-II error).

For the sake of completeness, one may notice that the variable error was significantly higher for the left than for the right resting point (L:  $7110 \pm 4696$  mm<sup>2</sup>; R:  $5404 \pm 3088$  mm<sup>2</sup>;  $F_{1,9}=5.61$ ;  $P < 0.05$ ). No interaction was observed between the two experimental factors ( $F_{1,9}=0.58$ ;  $P > 0.45$ ).

#### *Subjects' performance did not vary over time*

Because only two hand positions were considered and each was repeated 12 times, implicit learning may potentially explain the absence of drift observed in the present experiment. If such is the case, one may expect the absolute distance between the no-delay

and delay mean locations to have decreased in the second half of the experiment with respect to the first half. To test this prediction, a two-way ANOVA with repeated measures was performed (hand resting point: left, right; time: first half, second half). Results indicated that the distance between the delayed and non-delayed localizations did not change over time (main effect  $P > 0.90$ ; interaction  $P > 0.10$ ). For the left resting point, the spatial distance between the no-delay and delay conditions increased slightly in the second half of the study (18.4 mm vs. 22.2 mm). It decreased by a comparable amount for the right resting point (16.0 mm vs. 12.7 mm). The same stability was observed for the variable error. If the subjects had progressively memorized two discrete hand positions, one may have expected the variable error to decrease in the second part of the study irrespective of the delay factor. To test this prediction, variations of the surface of the 95% confidence ellipse were compared as a function of time (first vs. second half of the study) for each resting point, using a two way ANOVA with repeated measures (time, resting point). Results indicated that neither the main effect ( $P > 0.90$ ) nor the interaction ( $P > 0.80$ ) involving the time factor reached the significance level. A slight increase of the variable error was observed in the second half of the study for the left resting point ( $7025$  mm<sup>2</sup> vs.  $7359$  mm<sup>2</sup>). A decrease was observed for the right resting point ( $5324$  mm<sup>2</sup> vs.  $5140$  mm<sup>2</sup>). All together, these results suggest that the absence of proprioceptive drift observed in the present study was not related to a memorization process.

#### Discussion

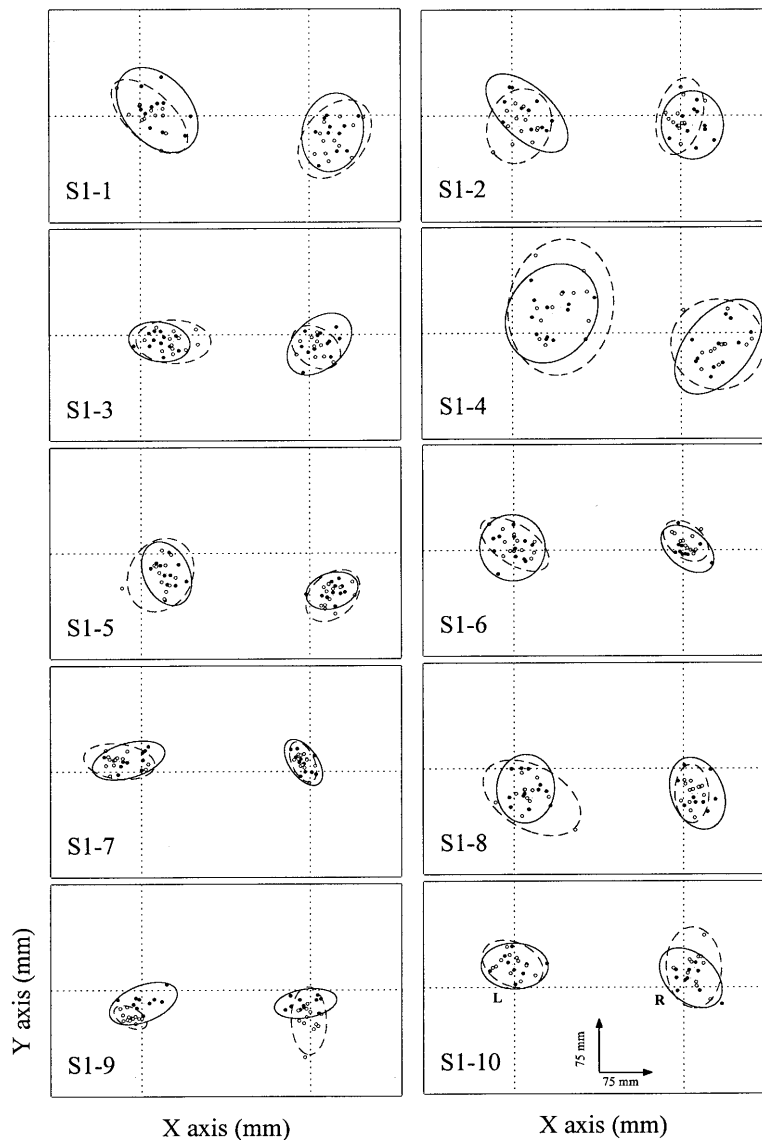
The main observation of this first experiment was that introducing a 10-s delay between the arm positioning and the localization process did not cause the mean systematic or mean variable error to change significantly. This result argues against the hypothesis that proprioception quickly drifts or degrades over time, contrasting with earlier findings in humans (Paillard and Brouchon 1968; Craske and Crawshaw 1975; Velay 1984; Wann and Ibrahim 1992). Potential explanations that may account for this discrepancy are considered below.

One may argue that our failure to observe a time-related degradation of the ability to locate the static hand resulted from the fact that the 10-s resting period was not long enough to allow proprioception to drift. This hypothesis is unlikely, however, considering that 10 s has been repeatedly found to be a sufficient delay to observe a degradation of the ability to estimate the hand location (Bowditch and Southard 1880; Paillard and Brouchon 1968; Wann and Ibrahim 1992).

To explain the absence of effect of the delay factor in the present experiment, one may also suggest that the reference condition was not a zero-delay condition, but a short-delay condition. Indeed, as shown in the Results section, the actual delay elapsed between the extinction of the light and the positioning of the spot was not equal to zero, but to almost 10 s. This "additional" delay involved two components:

1. The time elapsed between the extinction of the light and the positioning of the hand at the resting point. Because propriocep-

**Fig. 3** Hand-location estimation distributions and 95% confidence ellipses for all subjects (S1-1 to S1-10) and the two resting positions (intersection of the dotted straight lines), under the delay (white circles, dashed ellipses) and no-delay (black circles, continuous ellipses) conditions (experiment 1)



tion is not supposed to drift when the subject actively moves his arm (Wann and Ibrahim 1992), this component should not affect our results. Indeed, in the present study, the experimenter only guided the subject's hand, forcing him to actively mobilize his arm to reach the resting point (see methods).

2. The time used by the subject to position the spot. As shown in the literature, the so-called proprioceptive drift is progressive and does not cease within the first few seconds following visual occlusion (e.g., Paillard and Brouchon 1968; Velay 1984; Wann and Ibrahim 1992). Wann and Ibrahim (1992, p 165) observed, for instance, "a steady linear drift" from 0 to 120 s. Therefore, it does not seem that the time required to position the spot, or more generally the time elapsed between the extinction of the light and the actual estimation of the hand location, can account for our inability to observe a proprioceptive drift during visual occlusion. Further arguments supporting this conclusion will be provided in the second and third experiments.

In contrast to the previous explanations, the "proprioceptive drift" observed in several earlier studies may reflect the existence of transient cues available only in the no-delay condition (see introduction for details). This occurs, for instance, when the subject is able to evaluate the magnitude of the positioning movement of the target hand (Paillard and Brouchon 1968; Craske and Crawshaw

1975) or when vision is turned off just before the matching procedure (Wann and Ibrahim 1992).

In a comprehensive study, Horch et al. (1975) attempted to determine the effect of visual occlusion on the ability to estimate the position of an immobilized limb. At the beginning of each trial, one of the subject's knees was positioned at a predetermined angle. After a various delay, instruction was given to match the angle of the "reference" knee with the contralateral leg. Results failed to indicate any significant change in matching performance with time, even for 180-s delays. This observation is compatible with the results of other studies involving recall paradigms (DelRey and Lichter 1971; Lee and Kelso 1979). As shown by Horch et al. (1975), however, the ability of human subjects to remember a particular position of the knee is quite impressive. These authors compared two experimental conditions. In the first condition, the right knee was positioned at a particular angle for 1 min, after which the subject was instructed to match the right-knee's angle with the contralateral leg. In the second condition, the right knee was held at a "reference" angle for 15 s and then returned to its resting posture. After 45 s, the subject was required to match the reference angle with the left leg. Results indicated that "none of the subjects showed significant differences in mean match angle between direct comparison and memory matches". This amazing result, which the authors replicated for the shoulder joint, indicates

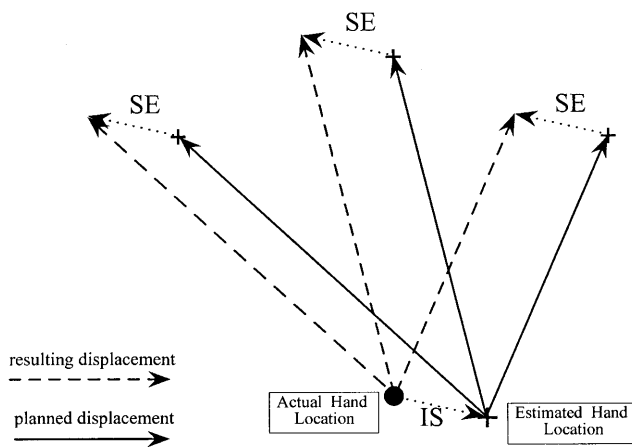
that the interpretation of perceptual experiments reporting a proprioceptive drift is delicate. It is our opinion that the confounding effect of memory and attention may explain part of the contrasting observations reported in the literature. To overcome this confound, we tested for the existence of a proprioceptive drift in a purely motor experiment, for which the subjects did not pay attention to the hand initial location.

## Experiment 2

Converging evidence suggests that pointing errors reflect, in part, systematic biases in the estimation of the initial hand location (Prablanc et al. 1979; Bock and Eckmiller 1986; Jaric et al. 1992; Bock and Arnold 1993; Rossetti et al. 1994, 1995; Desmurget et al. 1995, 1997b; Ghilardi et al. 1995; Vindras et al. 1998; for a review, see Desmurget et al. 1998). As an illustration, consider the experiment carried out by Rossetti et al. (1995). These authors required human subjects to point toward visual targets without vi-

sion of their moving limb. In a first condition, the hand was seen, at rest, through prisms that created a visual displacement. The target was presented outside the shifted field and, thus, was seen normally. In a second condition, the prism was replaced by an ordinary lens, and both the hand and the target were seen normally. Comparison between the two conditions showed that the visual displacement of the fingertip position prior to movement induced a systematic bias of the movement end-point, in a direction opposite to the initial visual shift. This observation agrees with a recent study in which human subjects were required both to estimate the position of their right hand at two different locations (localization) and to perform horizontal, visually directed pointing, with the right hand, from these two locations (Vindras et al. 1998). When the end-point errors observed in the reaching task were compared with the systematic biases observed in the localization task, a strong correlation was found, indicating that motor errors reflected, in part, systematic biases in the perception of the initial hand position.

The effect of incorrectly evaluating the initial location of the hand has been found to alter three main movement parameters, namely the movement initial direction (Ghilardi et al. 1995; Rossetti et al. 1995), the end-point-accuracy (Bock and Eckmiller 1986; Jaric et al. 1992; Rossetti et al. 1995; Desmurget et al. 1997b; Vindras et al. 1998), and the end-point variability (Prablanc et al. 1979; Rossetti et al. 1994; Desmurget et al. 1995, 1997b). As a consequence, if proprioception drifts, one may expect these parameters to vary when a delay is introduced between the positioning of the hand and the presentation of the target. The main aim of the present experiment was to examine this prediction. Because most of the studies showing a relation between movement accuracy and the ability to estimate the initial hand position involve planar movements, we chose to study a planar pointing task. The fact that these movements follow straight-line paths in Cartesian space (Morasso 1981; Gordon et al. 1994; Desmurget et al. 1997a, 1999b; for a review, see Desmurget et al. 1998) should simplify the interpretation of potential biases observed when a resting delay is imposed prior to movement onset (Ghilardi et al. 1995; Vindras et al. 1998). This point is illustrated in Fig. 4, which summarizes the main predictions attached to the present experiment.



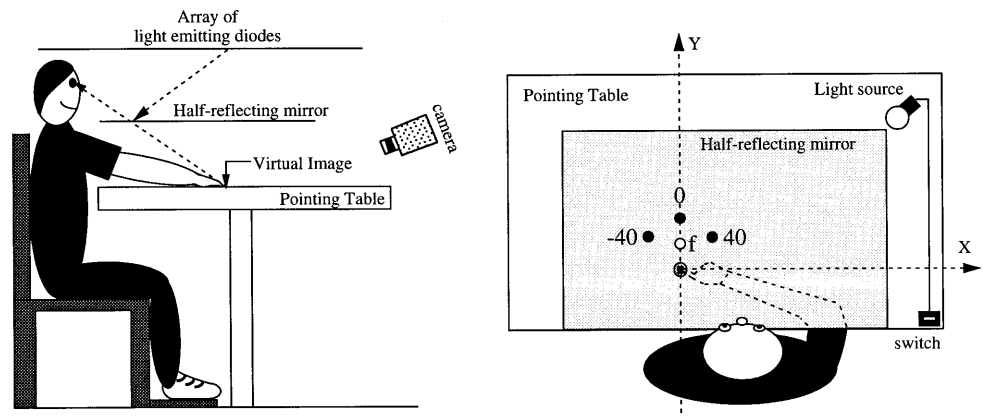
**Fig. 4** Planar movements have been found to follow a straight line path in the Cartesian space (see Desmurget et al. 1998 for a review). Consequently, when joint kinematics are computed on the basis of an erroneous representation of the hand location, movement end-points are expected to exhibit a systematic-error vector ( $SE$ ), similar in amplitude and opposite in direction to the initial shift ( $IS = -SE$ ; Vindras et al. 1998). If proprioception drifts,  $IS$  will vary, producing significant changes in  $SE$ . Note that an erroneous estimation of the initial hand location should also affect movement accuracy if the trajectory is not controlled in the Cartesian space. In this case, however, the systematic error vector is expected to vary with the target eccentricity (Desmurget et al. 1999b)

## Materials and methods

### Apparatus and procedure

Seven normal right-handed volunteers, aged from 19 to 31 years, participated in this experiment. They were different from the ones involved in the first experiment. Subjects were all devoid of visual deficits and naive about the purpose of the study. The experimental device is illustrated in Fig. 5. It consisted of a horizontal table, in front of which the subject was seated comfortably. The height of the table was adjusted to be level with the lower part of the subject's sternum. An array of red light-emitting diodes (LEDs) and a

**Fig. 5** Schematic representation of the experimental apparatus used in experiments 2 and 3. For explanation of abbreviations etc., see text



half-reflecting mirror were suspended over the pointing surface. The subjects saw the virtual images of small dots (pointing targets) through the mirror, in the plane of the pointing table (when the light was off, subjects could never cover the diodes, which prevented an indirect estimation of the movement final error). Three targets were used. They were located on a circle (radius: 12.5 cm). Their angular excursions, defined with respect to the sagittal axis, were, respectively, 40° to the left (-40°), 0°, and 40° to the right (+40°). The hand starting position was located at the center of the target circle (C). In order to allow the right arm to rest on the table in a totally passive position, the point C was set 20 cm in front of the subjects' left shoulder. A visual fixation point (green LED) was defined 6 cm in front of C, along the sagittal axis. During the experiment, the subjects were asked to hold a stylus as close as possible to its tip. They were instructed to leave the tip of the stylus in contact with the table. Movements of the right hand were recorded with an Elite system at a frequency of 100 Hz.

A typical trial involved 6 steps:

1. The light was turned on to update representation of the hand location.
2. The experimenter guided the subject's hand to the resting point. As in the first experiment, this positioning movement was not totally passive inasmuch as the subject had to provide the motor energy necessary to move the guided arm. The light remained on until the tip of the stylus used to point was within 4 cm from the required position (i.e., the subject did not see his hand at the starting point or during the movement). Although not recorded in this experiment, the time elapsed between the extinction of the light and the actual positioning of the hand at rest was estimated to be around 2 s.
3. Either immediately after the positioning of the hand (no-delay trial) or after a 15-s delay (delay trial), a tone was given and the fixation point was turned on, indicating to the subject to be ready to point.
4. After a fixation period (1 s), the fixation point was turned off and the target was presented. The subject was instructed to "look and point" quickly to the target. He/she was required to avoid corrections and to reach the target with a single uncorrected movement. Vision of the moving limb was not allowed. Velocity was stressed to prevent unconscious on-line trajectory adjustments from occurring (Prablanc and Martin 1992; Desmurget et al. 1999a). At the beginning of the experiment, subjects were trained briefly with a metronome to perform movements shorter than 350 ms.
5. After completion of the pointing, the experimenter moved the subject's hand about 30 cm away from its current location to prevent the subject from visually comparing the actual hand position with the position where he/she thought the hand to be.
6. The light was turned on again.

In one single session, each subject performed 60 movements (three targets  $\times$  two delays  $\times$  ten repetitions). During the session, the three targets and the two delays were randomly intermixed. It is worth mentioning, here, that the labels "no-delay" and "delay" were used for the sake of simplicity despite the existence of a short delay between the extinction of the light and the movement onset. This delay (~3.5 s) was equal to the fixation period (1 s) plus the reaction time (~300 ms) plus the time elapsed between the extinction of the light and the positioning of the hand at the starting point (~2 s).

#### Data analysis

The position signal was filtered at 10 Hz with a zero-phase finite impulse response (FIR) filter, using 33 coefficients. Velocity was computed from the filtered position signal using a least-square second-order polynomial method (window  $\pm 4$  points). The same method was used to compute the acceleration from the velocity signal. The onset and the end of the movement were computed automatically using the following thresholds: hand velocity=8 cm/s,

hand acceleration=150 cm/s<sup>2</sup> (these values were chosen to fit with the values obtained from a visual windowing).

An orthogonal frame of reference was defined for data analysis (Fig. 5). This frame was centered on the starting point C. The y axis was sagittal and oriented forward; the x axis was fronto-parallel and oriented rightward. Four parameters were considered:

1. The movement linearity. This parameter was computed using an index initially proposed by Atkeson and Hollerbach (1985). For each movement, the equation of the straight line joining the start and end points was defined. The largest deviation ( $d$ ) of arm trajectory from that line was then determined. The movement linearity index was defined as the ratio of  $d$  to the length of the line connecting the start and end-points of the movement. This parameter was mainly computed in order to determine whether hand-path modifications occurred during the course of the "delayed" movements. Indeed, one may not exclude that an erroneous estimation of the initial hand location can be partially updated during the movement, leading to a modification of the hand trajectory (Prablanc and Martin 1992; Desmurget et al. 1999a). In support of this possibility, it was suggested that position sense (which involves static proprioception) and movement sense (which involves dynamic proprioception) might represent functionally distinct entities (Clark et al. 1985; Matthews 1988).
2. The hand initial acceleration vector. It was defined as the acceleration vector at the instant of peak acceleration (i.e., around 100 ms after movement onset in the present experiment; see results). This temporal landmark was chosen on the basis of psychophysical experiments showing that hand trajectory is not yet affected by on-line control feedback loops at the instant of peak acceleration (Prablanc and Martin. 1992; Carnahan et al. 1993).
3. The systematic error. Systematic error was defined as the vector joining the mean movement end-point to the target. The components of the systematic-error vector were named SE<sub>x</sub> (fronto-parallel axis) and SE<sub>y</sub> (sagittal axis).
4. The variable error. It was defined, for each subject and each target, as the surface of the 95% confidence ellipse of the end-point distribution (see experiment 1).

In order to test the influence of the experimental factors on both the movement linearity and the end-point variability, univariate ANOVAs with repeated measures were performed. For the systematic errors and the initial acceleration vector, multivariate ANOVAs with repeated measures were computed. In this latter case, the  $F$  value was determined from Wilk's lambda, using Rao's approximation (Maxwell and Delaney 1990). For both the multivariate and the univariate analyses, the repeated-measures factors were: "delay" (two levels: no-delay, delay), and "target" (three levels: -40°, 0°, +40°). Threshold for statistical significance was set at 0.05. The Duncan significant difference test was used for post-hoc comparisons of the univariate means (Winer 1971). For the linearity index, the systematic error, and the initial movement direction, additional intra-individual analyses were performed to ascertain that non-significant "between-subjects" analyses did not result from compensating significant individual changes (see experiment 1). For the within-subject analyses, two-way MANOVAs were performed with "delay" and "target" as experimental factors. To test whether intra-subject analyses globally confirmed or rejected the  $H_0$  hypothesis for systematic errors, a Kolmogorov-Smirnov test was performed (experiment 1 confirmed that this test was more powerful, and statistically more justified, than a MANOVA with subjects as a factor).

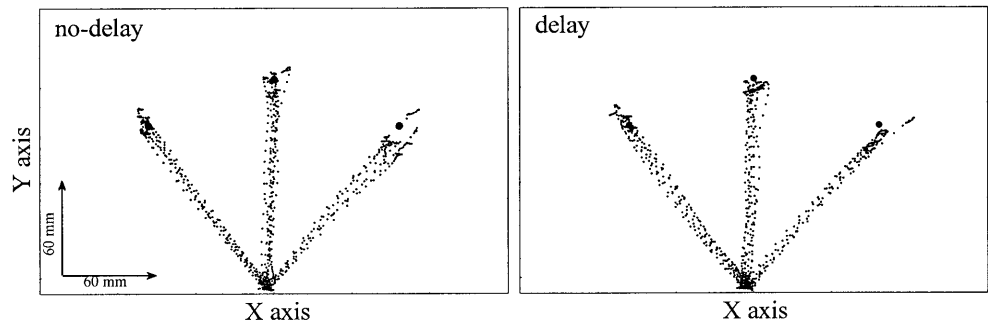
#### Results

##### General observations

Subjects were asked, at the end of the experiment, about what, according to their view, was the purpose of the study. Three said that they had no idea, while the others evoked factors like the ability to control the movement in the dark, the ability to get used to the



**Fig. 6** Hand paths exhibited by a representative subject under the no-delay (left panel) and delay (right panel) conditions (experiment 2)



dark, or the effect of waiting on reaction time. None of the subjects reported, even elusively, that the main aim of the experiment might have been to test whether the ability to estimate the location of the unseen hand, at rest, degrades over time. The subjects were also required to evaluate if there was one or several starting points. To our surprise they all estimated that several different starting locations were used (subjects' answers ranged from three to nine starting points), confirming that static proprioception fails to give accurate information about hand position (Ghilardi et al. 1995; Desmurget et al. 1997b; Vindras et al. 1998). When told that there was only one starting location, most did not want to believe it. Finally, the subjects were informed about the real purpose of the study. Then, they were asked if they used specific strategies during hand positioning. Only one (S2-4) gave a positive answer, reporting that he tracked his hand visually after the light was turned off.

#### *Kinematic parameters*

The mean reaction time was equal to 288 ms ( $\pm 75$  ms) for the no-delay condition and to 285 ms ( $\pm 75$  ms) for the 15-s delay condition. Neither the main effects nor the interaction between the experimental factors was found to reach the statistical threshold (all  $P > 0.25$ ).

The mean movement duration was shorter than 400 ms for all subjects. It was not statistically different between the delay and no delay conditions (delay:  $336 \pm 37$  ms, no-delay:  $341 \pm 32$  ms;  $F_{1,6} = 0.99$ ,  $P > 0.35$ ). Time to peak acceleration occurred, on average, around 100 ms. Like movement duration, this parameter was insensitive to the delay factor (delay:  $100 \pm 10$  ms, no-delay:  $102 \pm 8$  ms;  $F_{1,6} = 0.76$ ,  $P > 0.40$ ). No interaction was observed between the delay and target factors for the movement duration or the time to peak acceleration ( $F_{2,12} < 0.21$ ,  $P > 0.80$ ).

#### *The resting period did not significantly influence the movement curvature*

Figure 6 shows individual movements performed by a representative subject (S2-2) to the three targets in both the no-delay (left panel) and the delay condition (right panel). As shown in the figure, movement paths were essentially straight, irrespective of the movement direction. Between-subjects statistical analyses indicated that the mean linearity index was not significantly different in the delay and no-delay conditions ( $0.036 \pm 0.009$  vs.  $0.038 \pm 0.009$ ;  $F_{1,6} = 1.59$ ,  $P > 0.25$ ). The interaction between the experimental factors did not reach statistical significance ( $F_{2,12} = 1.12$ ,  $P > 0.35$ ). This indicates that the subjects did not adjust the movement trajectory in the delay condition to adapt for the erroneous motor command that may have resulted from a biased estimation of the initial hand location. A slight, but significant variation of the path curvature was observed as a function of the movement eccentricity ( $-40^\circ$ :  $0.037 \pm 0.007$ ,  $0^\circ$ :  $0.043 \pm 0.008$ ,  $+40^\circ$ :  $0.030 \pm 0.005$ ;  $F_{2,12} = 10.99$ ,  $P < 0.005$ ).

Intra-individual comparisons confirmed the absence of effect of the delay factor on the movement curvature for all the subjects

except S2-4 (for both the simple effect of the delay factor and the interaction effect, all  $P > 0.35$ ). For S2-4, a significant interaction was observed between the delay and target factors ( $F_{2,54} = 6.00$ ,  $P < 0.005$ ). Post-hoc analysis performed with respect to this interaction showed that a significant increase of the path curvature was observed in the delay condition for the  $+40^\circ$  target ( $0.026$  vs.  $0.045$ ; Duncan significant difference test,  $P < 0.002$ ). This suggests that some path corrections may have occurred, for S2-4, as a result of a modification of the perceived hand location during the initial waiting period.

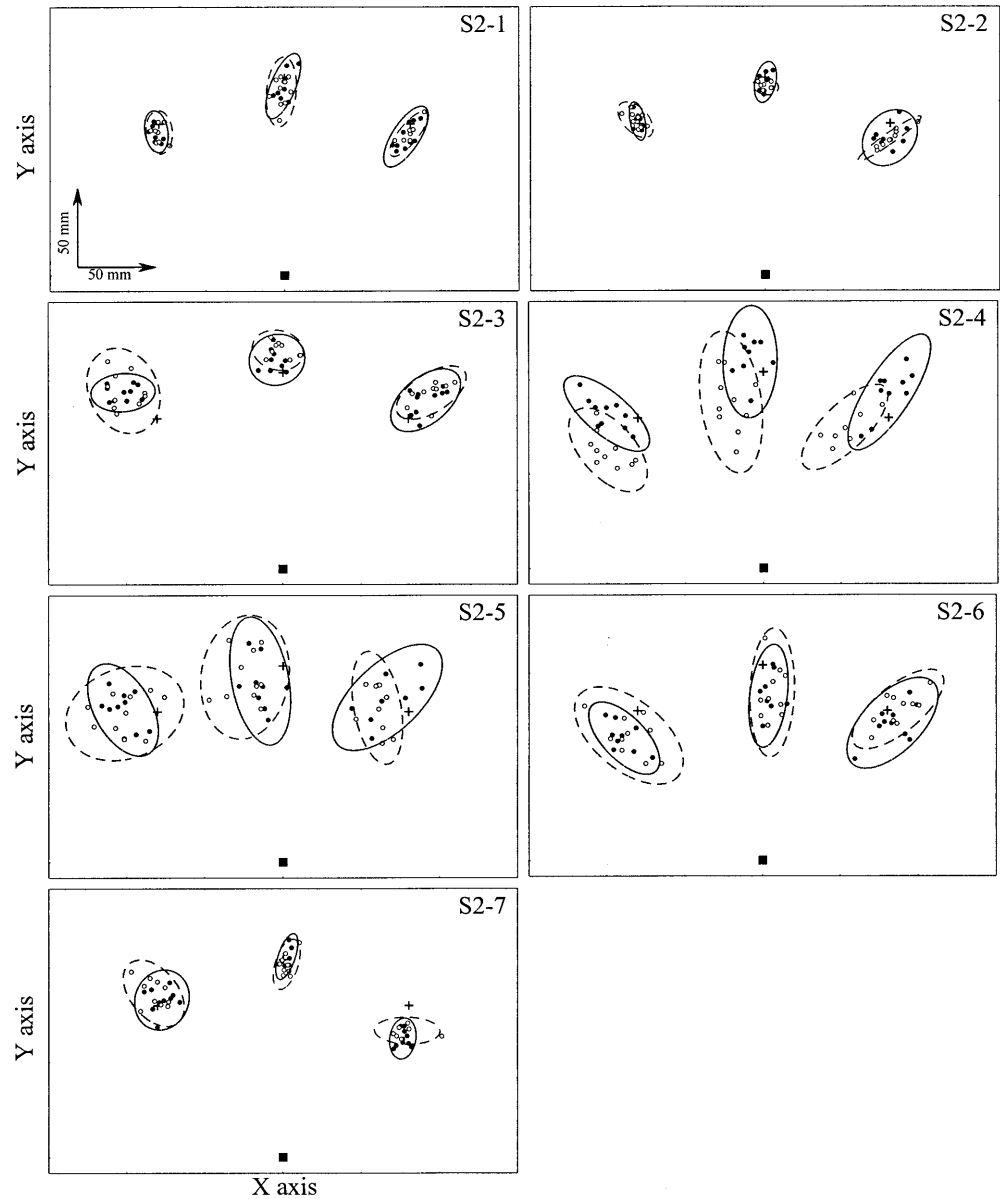
#### *The systematic pointing errors did not vary significantly as a function of the resting delay*

The pattern of systematic errors varied consistently from subject to subject. As displayed in Fig. 7, while some subjects were quite accurate (e.g., S2-1), others consistently overshoot (e.g., S2-3) or undershoot (e.g., S2-6) the targets. Between-subject analyses did not reveal any significant variation of the systematic errors as a function of either the delay ( $F_{2,5} = 0.68$ ;  $P > 0.50$ ) or the target ( $F_{4,3} = 3.01$ ;  $P > 0.15$ ) factors. No interaction was observed ( $F_{4,3} = 1.80$ ;  $P > 0.30$ ).

Intra-individual analyses confirmed, for all the subjects but one, the absence of effect of the delay factor on the systematic errors. As reported in Table 2, only S2-4 exhibited a significant difference in the end-point location when a waiting period was imposed between the hand positioning and the pointing. For this subject, the mean end-point tended to drift toward the left and in the direction of the body (Fig. 7). It should be mentioned that an interaction was observed for another subject (S2-7) between the target and delay factors. With respect to this result, however, three points are worth noting. First, post-hoc analyses indicated that the x and y end-point coordinates were not significantly different for the delay and no-delay conditions given a target location (Duncan significant difference test:  $P > 0.09$ ). Second, a potential effect of the delay factor for S2-7 was not confirmed for the other parameters tested in this experiment, in contrast to what was observed for S2-4. Third, a strict approach would impose that the statistical threshold be corrected for multiple comparison in the context of within-subject analyses (Bonferroni adjustments; Maxwell and Delaney 1990). While the delay-related effect observed for S2-4 would survive such correction, the delay-target interaction observed for S2-7 would not.

The absence of general effect of the delay factor was corroborated by further analyses showing that the individual  $F$ -tests were distributed according to a  $F(2,43)$  statistic, in agreement with the hypothesis that localizations are independent of the delay factor (Kolmogorov-Smirnov test,  $P > 0.40$ ). This result can be graphically apprehended in Fig. 7. As shown in this figure, the pointing distributions related to the delay and no-delay conditions greatly overlap in all subjects but S2-4, confirming that there was no global trend for a modification of the end-point accuracy as a function of the delay factor.

**Fig. 7** End-point distributions and 95% confidence ellipses for all subjects (S2-1 to S2-7) and targets eccentricities (cross), under the delay (white circles, dashed ellipses) and no-delay (black circles, continuous ellipses) conditions (experiment 2). Black squares at the bottom of each panel represent the movement starting point



**Table 2** Intra-individual MANOVAs involving the systematic errors (experiment 2). Significant effects are represented in **bold characters** ( $P < 0.05$ , uncorrected for multiple comparisons). The  $F$  values were determined from the Wilk's lambda, using the Rao's approximation (Maxwell and Delaney 1990)

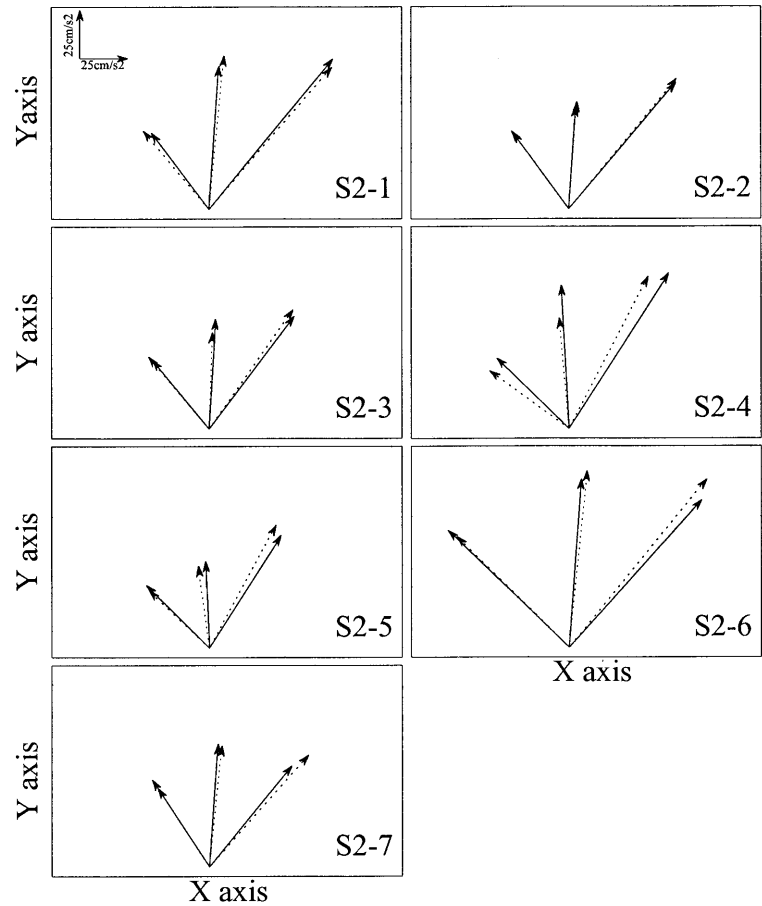
Subject	Delay $F(2,53)$	Target location $F(4,106)$	Delay $\times$ location $F(4,106)$
S1	$F=0.52$ ( $P>0.60$ )	$F=0.38$ ( $P>0.80$ )	$F=0.53$ ( $P>0.70$ )
S2	$F=0.58$ ( $P>0.55$ )	<b><math>F=8.01</math> (<math>P&lt;0.0001</math>)</b>	$F=0.83$ ( $P>0.50$ )
S3	$F=2.22$ ( $P>0.10$ )	<b><math>F=30.6</math> (<math>P&lt;0.0001</math>)</b>	$F=0.40$ ( $P>0.80$ )
S4	<b><math>F=33.8</math> (<math>P&lt;0.0001</math>)</b>	<b><math>F=3.54</math> (<math>P&lt;0.01</math>)</b>	<b><math>F=4.99</math> (<math>P&lt;0.002</math>)</b>
S5	$F=1.50$ ( $P>0.20$ )	<b><math>F=2.67</math> (<math>P&lt;0.04</math>)</b>	$F=0.85$ ( $P>0.45$ )
S6	$F=1.35$ ( $P>0.25$ )	<b><math>F=8.22</math> (<math>P&lt;0.0001</math>)</b>	$F=0.24$ ( $P>0.90$ )
S7	$F=0.51$ ( $P>0.60$ )	<b><math>F=26.7</math> (<math>P&lt;0.0001</math>)</b>	<b><math>F=2.85</math> (<math>P&lt;0.03</math>)</b>

*The resting period did not significantly influence the initial acceleration vector*

Neither the main effect ( $F_{2,5}=0.40$ ,  $P>0.65$ ) nor the interaction involving the delay factor ( $F_{4,3}=1.61$ ,  $P>0.35$ ) were found to reach the statistical significance threshold, showing that movement initial acceleration did not significantly vary when the subjects had to hold their hand in a static position before pointing. Intra-indi-

vidual comparisons confirmed this result for all the subjects but one (Fig. 8). As for the systematic errors, only S2-4 was found to exhibit a significant variation in the initial acceleration vector when a waiting period was imposed between the hand positioning and the pointing ( $F_{2,53}=12.20$ ,  $P<0.0001$ ). For this subject, the initial acceleration vector was, in particular, rotated to the left.

**Fig. 8** Acceleration vector at time to peak acceleration ( $\approx 100$  ms) for the delay (*dotted line*) and no-delay (*continuous line*) conditions (experiment 2). S2-1 to S2-7 Individual subjects



*The variable error did not increase significantly with the resting delay*

The surface of the 95% confidence ellipsoid characterizing the variable error was found to be slightly higher when a delay was introduced between the arm positioning and the pointing movement (no-delay:  $1170 \pm 783$  mm<sup>2</sup>; delay:  $1385 \pm 1072$  mm<sup>2</sup>). As shown by the ANOVA, this difference did not reach the statistical threshold ( $F_{1,6}=3.75$ ;  $P>0.10$ ). This indicates that the dispersion of the movement end-points around its mean did not significantly increase in the delay condition. This result is illustrated in Fig. 7, which displays, for all subjects, the modification of the variable error ellipsoid as a function of the experimental conditions.

*Pointing accuracy did not vary over time*

Because only three target positions were considered and each was reached ten times, implicit learning may potentially explain the absence of drift observed in the present experiment. As in the first experiment, if such is the case, one may expect the absolute distance between the no-delay and delay mean end-point location to decrease in the second half of the study with respect to the first half. To test this prediction a two-way ANOVA with repeated measures was performed (target location:  $-40^\circ$ ,  $0^\circ$ ,  $+40^\circ$ ; time: first half, second half). Results indicated that the distance between the delayed and non-delayed localizations did not change over time (interaction and main effect  $P>0.15$ ). On average, the spatial distance between the no-delay and delay conditions was 10.0 mm for the first half of the experiment and 8.7 mm for the second half. The same stability was observed for the variable error. As shown by a two-way ANOVA (target location, time), the surface of the 95% confidence ellipse was not significantly smaller in the second

than in the first part of the study ( $1537$  mm<sup>2</sup> vs.  $1024$  mm<sup>2</sup>; interaction and main effect  $P>0.10$ ). All together, these results suggest that the absence of proprioceptive drift observed in the present experiment was not related to the fact that the subjects learned and memorized the three target locations.

#### Discussion

The main observation related to this experiment was that introducing a 15-s delay between arm positioning and target presentation did not cause the mean movement accuracy to change. This result does not support earlier observations showing that static proprioception quickly drifts in the absence of visual cues (Paillard and Brousson 1968; Craske and Crawshaw 1975; Velay 1984; Wann and Ibrahim 1992). If the proprioceptive estimation of the hand location had deteriorated rapidly in the dark, both the movement accuracy and the movement kinematics would have been expected to vary (Prablanc et al. 1979; Bock and Eckmiller 1986; Jaric et al. 1992; Bock and Arnold 1993; Rossetti et al. 1994, 1995; Desmurget et al. 1995, 1997b; Ghilardi et al. 1995; Vindras et al. 1998; for a review, see Desmurget et al. 1998).

In contrast with the previous generalization, it must be mentioned that a clear effect of the delay factor was observed for one subject. For S2-4, the mean movement end-point drifted toward the left and in the direction of the body (Fig. 4). This variation, as well as the significant leftward rotation of the initial acceleration vector, could be due to a rightward and forward change of the estimated location of the hand during the resting period (Rossetti et al. 1995; Vindras et al. 1998). However, it is not clear whether this observation supports the hypothesis of a "proprioceptive drift". On the one hand, indeed, the change in movement characteristics observed for S2-4 might indicate that proprioception had drifted dur-

ing the waiting period, which would suggest that, even if the phenomenon of “proprioceptive drift” does not represent a general rule, it can occur in some cases. On the other hand, however, the end point shift exhibited by S2-4 could have resulted from a specific strategy providing transient additional information in the no-delay condition. When questioned at the end of the experiment, this subject reported that he tracked his index fingertip with his eyes during the positioning stage, after extinction of the light. This strategy was not reported by any other subjects. Thus, the change in movement accuracy observed for S2-4 is also compatible with the existence of a progressive deterioration of the eye-position signals during the initial delay.

Putting aside the indecisive subject S2-4, the absence of degradation of the hand location representation during visual occlusion has potential implications for knowing how viewing the hand at rest improves pointing accuracy. This phenomenon was first reported by Prablanc et al. (1979), who compared the final precision of visually directed movements under two different conditions. In the first condition, vision of the hand was never allowed (FOL: full open loop). In the second condition, vision of the hand was allowed only in static position prior to movement onset (DOL: dynamic open loop). Results showed that movement accuracy was significantly better in DOL than in FOL. This observation, which was subsequently reproduced by several authors (Rossetti et al. 1994; Desmurget et al. 1995, 1997b; Ghilardi et al. 1995; Vindras et al. 1998), was commonly interpreted in terms of recalibration of the proprioceptive space by the visual input (Prablanc et al. 1979; Jeannerod 1988; Wann and Ibrahim 1992; Rossetti et al. 1994). Our data do not agree with this view. Indeed, we did not find the proprioceptive signal to drift or degrade quickly during visual occlusion. Considering this negative result, one may evoke two hypotheses to account for the fact that viewing the hand at rest improves movement accuracy. The first one suggests that vision and proprioception are combined to build a bimodal representation of the hand location that is more accurate than each of the unimodal representations alone (Desmurget et al. 1995; Rossetti et al. 1995). Evidence supporting this view was provided by van Beers et al. (1996), who required human subjects to estimate the location of their unseen hand using visual, proprioceptive, or visual-proprioceptive information. Results showed that the variance of the estimated hand position was significantly smaller in the bimodal situation where both vision and proprioception could be used. A possible physiological underpinning for this “enhanced multimodal representation” was identified by Meredith and Stein (1986), who reported, in the cat, that neurons of the superior colliculus, which normally fire for visual or auditory stimuli, increase their discharge rate by a multiplicative factor when congruent auditory and visual stimuli are provided at the same time. The second, alternative hypothesis suggests that the positive effect of viewing the arm at rest is related to the simultaneous vision of the hand and target during movement planning (Blouin et al. 1993; Proteau and Marteniuk 1993; Rossetti et al. 1994; Redding and Wallace 1996). Consistent with this view is the recent finding that parietal cortex neurons provide an eye-centered representation of target position used to plan visual target reaching (Batista et al. 1999). Along this line of thinking, the degradation of pointing accuracy observed when the hand is not visible would not result from a proprioceptive drift, but rather from an inaccurate retinal representation of hand position.

### Experiment 3

In the previous experiments, the light remained on until the hand was 4 cm from the starting position. This leaves open the possibility that the subjects were able to extrapolate (consciously or not) the actual hand starting location from visual cues. It follows that the absence of proprioceptive drift observed in experiment 1 and 2 may rely on the stability of visual memory for spatial position. Conversely, however, it is also possible that the specific behavior exhibited by some subjects (e.g., S2-4) was related to a greater de-

pendence on a labile visual trace. The main aim of this experiment was to address this issue. The protocol was identical to the one used in the second experiment, except: (1) that subjects did not see their hand at the vicinity of the movement starting location, and (2) that the waiting period was increased from 15 to 20 s.

### Materials and methods

Six normal right-handed volunteers aged, from 17 to 32 years, participated in this experiment. They were different from the ones involved in the two first experiments. Subjects were all devoid of visual deficits and naive about the purpose of the study. The experimental device was the same as the one used in experiment 2, except that subjects pointed with a mouse whose bidimensional position movement was recorded at 200 Hz through a digitizing table. Another difference was related to the presence of an electronic switch controlling the light at the right side of the table (Fig. 5).

A typical trial involved 6 steps:

1. The subject was required to find the electronic switch in the dark using tactile information (without releasing the mouse), to turn the light on, and to look at his hand. The main aim of this manipulation was to update representation of the hand location before each trial.
2. The subject was requested to bring his hand back on the table.
3. The experimenter guided the subject's hand to the starting point. This positioning movement was not totally passive inasmuch as the subject had to provide the motor energy necessary to move the guided arm. Although not recorded in this experiment, the time elapsed between the extinction of the light and the actual positioning of the hand at rest was estimated at being around 4 s.
4. Either immediately after the positioning of the hand (no-delay trial) or after a 20-s delay (delay trial), a tone was given and the fixation point was turned on indicating to the subject to be ready to point.
5. After a fixation period (1 s), the fixation point was turned off and the target was presented. The subject was instructed to “look and point” quickly to the target. He/she was required to avoid corrections and to reach the target with a single uncorrected movement.
6. After completion of the movement, the target was turned off, indicating to the subject that he/she had to reach the switch to turn the light on.

In one single session, each subject performed 60 movements (three targets  $\times$  two delays  $\times$  ten repetitions). During the session, the three targets and the two delays were randomly intermixed. As in the second experiment, the labels “no-delay” and “delay” were used here, despite the existence of a short delay between the extinction of the light and the movement onset. This delay ( $\sim 5$  s) was equal to the fixation period (1 s) plus the reaction time ( $\sim 300$  ms) plus the time elapsed between the extinction of the light and the positioning of the hand at the starting point ( $\sim 4$  s).

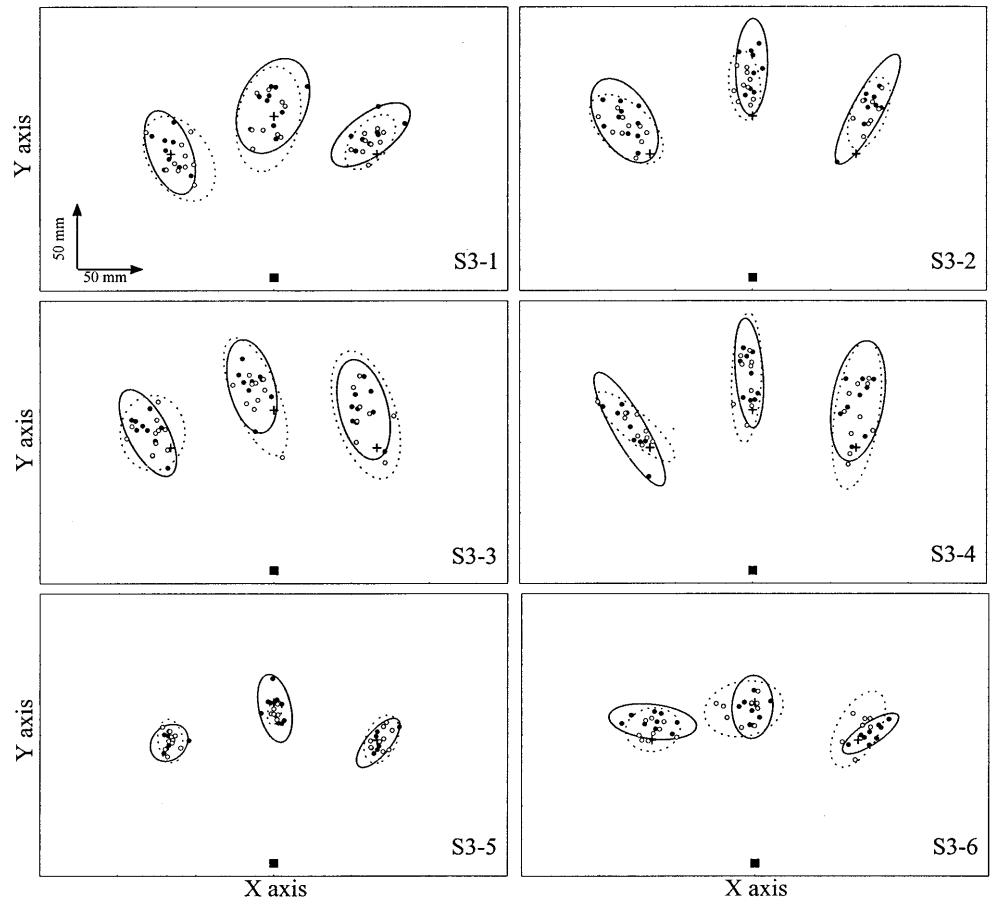
### Results

The results of this experiment were similar to the ones reported in the second experiment. Neither the reaction time (no-delay:  $420 \pm 129$  ms; delay:  $426 \pm 133$  ms) nor the movement duration (no-delay:  $414 \pm 61$  ms; delay:  $412 \pm 61$  ms) were significantly affected by the delay factor ( $F_{1,5} < 1.65$ ,  $P > 0.25$ ). No interaction was observed between the experimental factors ( $F_{2,10} < 2.5$ ,  $P > 0.10$ ).

Movement paths were nearly straight irrespective of the movement direction. Statistical analyses indicated that neither the mean linearity index (no-delay:  $0.038 \pm 0.014$ ; delay:  $0.036 \pm 0.011$ ;  $F_{1,5} = 0.31$ ,  $P > 0.60$ ) nor the initial acceleration vector ( $F_{2,4} = 1.70$ ,  $P > 0.25$ ) were significantly different in the no-delay and delay conditions. The interaction between the experimental factors did not reach statistical significance for these two parameters ( $P > 0.80$ ).



**Fig. 9** End-point distributions and 95% confidence ellipses for all subjects (S3-1 to S3-6) and targets eccentricities (cross), under the delay (white circles, dashed ellipses) and no-delay (black circles, continuous ellipses) conditions. Black squares at the bottom of each panel represent the movement starting point (experiment 3)



**Table 3** Intra-individual MANOVAs involving the systematic errors (experiment 3). Significant effects are represented in *bold characters* ( $P < 0.05$ , uncorrected for multiple comparisons). The  $F$  values were determined from the Wilk's lambda, using the Rao's approximation (Maxwell and Delaney 1990)

Subject	Delay $F(2,53)$	Target location $F(4,106)$	Delay $\times$ location $F(4,106)$
S1	$F=2.22$ ( $P > 0.10$ )	<b><math>F=4.34</math> (<math>P &lt; 0.003</math>)</b>	$F=0.72$ ( $P > 0.50$ )
S2	$F=2.61$ ( $P > 0.08$ )	<b><math>F=19.44</math> (<math>P &lt; 0.0001</math>)</b>	$F=0.88$ ( $P > 0.45$ )
S3	$F=0.78$ ( $P > 0.45$ )	<b><math>F=6.14</math> (<math>P &lt; 0.0002</math>)</b>	$F=0.25$ ( $P > 0.90$ )
S4	$F=0.36$ ( $P > 0.65$ )	<b><math>F=8.76</math> (<math>P &lt; 0.0001</math>)</b>	$F=0.75$ ( $P > 0.55$ )
S5	$F=0.31$ ( $P > 0.65$ )	$F=2.14$ ( $P > 0.08$ )	$F=0.51$ ( $P > 0.70$ )
S6	$F=2.05$ ( $P > 0.10$ )	<b><math>F=8.75</math> (<math>P &lt; 0.0001</math>)</b>	$F=1.61$ ( $P > 0.15$ )

Multivariate analyses did not reveal any significant variation of the systematic errors as a function of the delay factor ( $F_{2,4}=4.09$ ;  $P > 0.10$ ). No interaction was observed between the experimental factors ( $F_{4,2}=4.61$ ;  $P > 0.15$ ). As reported in Table 3, intra-individual analyses confirmed, for all subjects, the absence of delay-related effect on the systematic errors. The Kolmogorov-Smirnov statistic confirmed this point by showing that the individual  $F$ s were distributed according to a  $F(2,43)$  statistic, in agreement with the hypothesis that localizations are independent of the delay factor ( $P > 0.20$ ). This absence of effect of the delay factor is illustrated in Fig. 9.

The surface of the 95% confidence ellipsoid characterizing the variable error was found to be statistically identical in the no-delay and delay conditions (no-delay:  $1713 \pm 721$  mm<sup>2</sup>; delay:  $1821 \pm 1004$  mm<sup>2</sup>;  $F_{1,5}=0.29$ ;  $P > 0.60$ ), indicating that the dispersion of the movement end-points around its mean did not significantly increase in the delay condition. This result is illustrated in Fig. 9. No interaction was observed between the experimental factors for the variable error ( $F_{4,2}=0.22$ ;  $P > 0.80$ ).

Two-way ANOVAs with repeated measures (target location:  $-40^\circ$ ,  $0^\circ$ ,  $+40^\circ$ ; time: first half of the study, second half of the

study) did not provide evidence that an implicit learning process may explain our results. Neither the end-point variability (1561 mm<sup>2</sup> vs. 1369 mm<sup>2</sup>; interaction and main effect  $P > 0.35$ ) nor the distance between the delayed and non-delayed localizations (8.2 mm vs. 7.6 mm; interaction and main effect  $P > 0.75$ ) were different in the two parts of the study.

## Discussion

This experiment showed that the absence of drift observed in the two first experiments was not related to the ability of the subjects to use visual information to extrapolate the actual hand starting location in visual coordinates. This result was relatively predictable. Indeed, several studies have indicated that the memory for visual location is not stable over time. For instance, Chieffi and colleagues (Chieffi and Allport 1997; Chieffi et al. 1999) required human subjects to remember the location of a single visual stimulus over different delays and to recall its location by pointing to it with the tip of a stylus, with eyes closed. Two groups of subjects participated in the experiment. One group observed the target lo-

cations in the light, the other group in the dark. Results showed that the error in the remembered target location increased consistently over time delay for both groups. A similar result was reported by the Elliott group (Elliott and Madalena 1987; Elliott 1988), who observed that pointing accuracy decreased quickly when a delay was introduced between the presentation of the target and the go signal. A comparable observation was also reported by Thomson (1980, 1983), who required human subjects to walk to targets with their eyes closed. This author observed a significant degradation of the performance when the subjects were required to wait for 8 s before moving to the remembered target location.

## General discussion

Our capacity to estimate the position of our static hand in the dark relies on several heterogeneous sources of information, including proprioception, motor outflow, and the ability to memorize cues received at the time of hand positioning (Horch 1975; Jeannerod 1988; Matthews 1988). Because they overlooked the two latter factors, earlier studies concluded that the inability of human subjects to maintain a stable representation of the hand location in the dark resulted from a tendency of the proprioceptive signal to quickly drift when not afferented by vision (Paillard and Brouchon 1968; Craske and Crawshaw 1975; Velay 1984; Jeannerod 1988; Wann and Ibrahim 1992). The present experiments failed to support this conclusion. Indeed, we did not observe any trend in favor of the idea that position sense degrades during the first 20 s of visual occlusion when the subjects were forced to rely mainly on proprioception to evaluate the position of their hand.

Historically, the concept of proprioceptive drift was supported by the idea that the relation between vision and proprioception was both highly unstable and almost instantaneously modifiable. It was long assumed that proprioception was an "erratic sense" that quickly lost its calibration with respect to the external world when not afferented by vision (Jeannerod 1988). As noted by Craske and Crawshaw (1975, p 759), for instance, "it seems that kinesthesia manifests an underlying lability when information about the accuracy of its operation is not available. That limb position sense is exceedingly labile is no doubt; experiments with prisms have shown that kinesthesia can be easily modified when vision and kinesthesia are discordant". Although still common, this idea has been proved erroneous. It is true that prism adaptation quickly becomes complete. However, it is also established that aftereffects reflecting visual-proprioceptive realignment occur much slower than the behavioral adaptation itself (Radeau 1976; Kornheiser 1976). In some situations, the task-related adaptation has been reported to be complete without generating any sensory aftereffect (Taylor 1962). To explain this discrepancy, Redding and Wallace (1996) proposed to differentiate between two processes: (1) a *quick strategic process* that allows achieving the task through strategic control mechanisms (e.g., predictive feedforward adjustments, on-line feedback corrections); and (2) a *slow adaptive process* that actually realigns proprioception and vision and that needs detection of the sensory misalignment to occur. In

support of this dissociation, the authors observed that a large prism exposure (11.4°) did not generate any adaptive process when the subjects were pointing without receiving any error signal. In other words, despite a strong discrepancy between vision and proprioception, no recalibration was observed and the measured aftereffect was null. A compatible result was reported by Held and Hein (1958), who showed that viewing the hand in a static position, through a prism, during 3 min did not generate any adaptive realignment of the proprioceptive space with respect to the visual space. In view of these results, one may question the idea that proprioception represents a highly labile and unstable sense. Also, one may doubt that viewing the hand at rest during a few seconds (Wann and Ibrahim 1992; Rossetti et al. 1994) can recalibrate proprioception with respect to vision. However, one may not exclude the idea that longer periods of visual occlusion would result in a proprioceptive drift. Further investigations are required to address this possibility.

**Acknowledgements** We thank G.E. Alexander, G. Baud-Bovy and C. Prablanc for helpful discussions. We are also grateful to L. Payne for editing and commenting this manuscript.

## References

- Atkeson CG, Hollerbach JM (1985) Kinematic features of unrestrained vertical arm movements. *J Neurosci* 5:2318–2330
- Batista AP, Buneo CA, Snyder LH, Andersen RA (1999) Reach plans in eye-centered coordinates. *Science* 285:257–260
- Beers RJ van, Sittig AC, Denier van der Gon JJ (1996) How humans combine simultaneous proprioceptive and visual information. *Exp Brain Res* 111:253–261
- Block AM (1890) Expériences sur les sensations musculaires. *Revue Scientifique* 45:294–301
- Blouin J, Bard C, Teasdale N, Paillard J, Fleury M, Forget R, Lamarre Y (1993) Reference systems for coding spatial information in normal subjects and a deafferented patient. *Exp Brain Res* 93:324–331
- Bock O, Arnold K (1993) Error accumulation and error correction in sequential pointing movements. *Exp Brain Res* 95:111–117
- Bock O, Eckmiller R (1986) Goal-directed arm movements in absence of visual guidance: evidence for amplitude rather than position control. *Exp Brain Res* 62:451–458
- Bowditch HP, Southard WF (1880) A comparison of sight and touch. *J Physiol* 3:232–245
- Bridgeman B, Kirch M, Sperling A (1981) Segregation of cognitive and motor aspects of visual function using induced motion. *Percept Psychophys* 29:336–342
- Carnahan H, Goodale MA, Marteniuk RG (1993) Grasping versus pointing and the differential use of visual feedback. *Hum Mov Sci* 12:219–234
- Chieffi S, Allport DA (1997) Independent coding of target distance and direction in visuo-spatial working memory. *Psychol Res* 60:244–250
- Chieffi S, Allport DA, Woodin M (1999) Hand-centered coding of target location in visuo-spatial working memory. *Neuropsychologia* 37:495–502
- Clark FJ, Burgess RC, Chapin JW, Lipscomb WT (1985) Role of intramuscular receptors in the awareness of limb position. *J Neurophysiol* 54:1529–1540
- Craske B, Crawshaw M (1975) Shifts in kinesthesia through time and after active and passive movement. *Percept Mot Skills* 40:755–761
- DelRey P, Lichter J (1971) Accuracy in horizontal arm positioning. *Res Q* 42:150–155

- Desmurget M, Rossetti Y, Prablanc C, Stelmach GE, Jeannerod M (1995) Representation of hand position prior to movement and motor variability. *Can J Physiol Pharmacol* 73:262–272
- Desmurget M, Jordan M, Prablanc C, Jeannerod M (1997a) Constrained and unconstrained movements involve different control strategies. *J Neurophysiol* 77:1644–1650
- Desmurget M, Rossetti Y, Jordan M, Meckler C, Prablanc C (1997b) Viewing the hand prior to movement improves accuracy of pointing performed toward the unseen contralateral hand. *Exp Brain Res* 115:180–186
- Desmurget M, Pélisson D, Rossetti Y, Prablanc C (1998) From eye to hand: planning goal-directed movements. *Neurosci Biobehav Rev* 22:761–788
- Desmurget M, Epstein CM, Turner RS, Prablanc C, Alexander GE, Grafton ST (1999a) Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nat Neurosci* 2:563–567
- Desmurget M, Prablanc C, Jordan MI, Jeannerod M (1999b) Are reaching movements planned to be straight and invariant in the extrinsic space: kinematic comparison between compliant and unconstrained motions. *Q J Exp Psychol* 52A:981–1020
- Elliott D (1988) The influence of visual target and limb information on manual aiming. *Can J Psychol* 42:57–68
- Elliott D, Madalena J (1987) The influence of premovement visual information on manual aiming. *Q J Exp Psychol* 39A:541–559
- Ghilardi MF, Gordon J, Ghez C (1995) Learning a visuo-motor transformation in a local area of work space produces directional biases in other areas. *J Neurophysiol* 73:2535–2539
- Goodale MA, Haffenden A (1998) Frames of reference for perception and action in the human visual system. *Neurosci Biobehav Rev* 22:161–172
- Gordon J, Ghilardi MF, Ghez C (1994) Accuracy of planar reaching movements. 1. Independence of direction and extent variability. *Exp Brain Res* 99:97–111
- Held R, Hein A (1958) Adaptation of disarranged hand-eye coordination contingent upon reafferent stimulation. *Percept Mot Skills* 8:87–90
- Horch KW, Clark FJ, Burgess PR (1975) Awareness of knee joint angle under static conditions. *J Neurophysiol* 38:1436–1447
- Imanaka K, Abernethy B (1992) Cognitive strategies and short-term memory for movement distance and location. *Q J Exp Psychol* 45A:669–700
- Jaric S, Corcos D, Latash M (1992) Effects of practice on final position reproduction. *Exp Brain Res* 91:129–134
- Jeannerod M (1988) The neural and behavioural organization of goal-directed movements. *Motor Control: concepts and issues*. J Wiley, New York, pp 277–291
- Johnson RA, Wichern DW (1982) *Applied multivariate statistical analysis*. Prentice Hall, Englewood Cliffs
- Kornheiser AS (1976) Adaptation to laterally displaced vision: a review. *Psychol Bull* 83:783–816
- Lee WA, Kelso J (1979) Properties of slowly adapting joint receptors do not readily predict perception of limb position. *J Hum Mov Stud* 5:171–181
- Matthews PB (1988) Proprioceptors and their contribution to somatosensory mapping: complex messages require complex processing. *Can J Physiol Pharmacol* 66:430–438
- Maxwell SE, Delaney HD (1990) Designing experiments and analysing data. A model comparison perspective. Wadsworth, Belmont
- Meredith MA, Stein BE (1986) Visual, auditory and somatosensory convergence on cells in superior colliculus results in multi-sensory integrations. *J Neurophysiol* 56:640–662
- Mon-Williams M, Wann JP, Jenkinson M, Rushton K (1997) Synesthesia in the normal limb. *Proc R Soc Lond B Biol Sci* 264:1007–1010
- Morasso P (1981) Spatial control of arm movements. *Exp Brain Res* 42:223–227
- Paillard J, Brouchon M (1968) Active and passive movements in the calibration of position sense. In: Freedman SJ (ed) *The neuropsychology of spatially oriented behavior*. Dorsey Press, Illinois, pp 35–56
- Prablanc C, Martin O (1992) Automatic control during hand reaching at undetected two-dimensional target displacements. *J Neurophysiol* 67:455–469
- Prablanc C, Echallier JF, Jeannerod M, Komilis E (1979) Optimal response of eye and hand motor systems in pointing at visual target. II. Static and dynamic visual cues in the control of hand movement. *Biol Cybern* 35:183–187
- Proteau L, Marteniuk RG (1993) Static visual information and the learning and control of a manual aiming movement. *Hum Mov Sci* 12:515–536
- Radeau M (1976) L'adaptation au déplacement de l'espace visuel: revue critique. *Archives de Psychologie* 44:1–94
- Redding GM, Wallace B (1996) Adaptive spatial alignment and strategic perceptual-motor control. *J Exp Psychol Hum Percept Perform* 22:379–394
- Rock I (1966) *The nature of visual perception*. Basic, New York
- Rossetti Y (1998) Implicit short-lived motor representations of space in brain damaged and healthy subjects. *Conscious Cogn* 7:520–558
- Rossetti Y, Stelmach GE, Desmurget M, Prablanc C, Jeannerod M (1994) The effect of viewing the static hand prior to movement onset on pointing kinematics and accuracy. *Exp Brain Res* 101:323–330
- Rossetti Y, Desmurget M, Prablanc C (1995) Vectorial coding of movement: vision, proprioception or both? *J Neurophysiol* 74:457–463
- Siegel S (1956) *Nonparametric methods for the behavioral sciences*. McGraw-Hill, New York
- Taylor J (1962) *The behavioral basis of perception*. Yale University Press, New Haven
- Thomson JA (1980) How do we use visual information to control locomotion. *Trends Neurosci* 3:247–250
- Thomson JA (1983) Is continuous visual monitoring necessary in visually guided locomotion? *J Exp Psychol Hum Percept Perform* 9:427–443
- Velay JL (1984) *Sens de la position: les traitements sensori-moteurs des informations proprioceptives*. PhD dissertation, Université de Provence, Aix Marseille II
- Vindras P, Desmurget M, Prablanc C, Viviani P (1998) Pointing errors reflect biases in the perception of the initial hand position. *J Neurophysiol* 79:3290–3294
- Walsh WD, Russell DG, Imanaka K, James B (1979) Memory for constrained and preselected movement location and distance: effect of starting position and length. *J Mot Behav* 11:201–214
- Wann JP, Ibrahim SF (1992) Does limb proprioception drift? *Exp Brain Res* 91:162–166
- Welch RB, Widawski MH, Harrington J, Warren D (1979) An examination of the relationship between visual capture and prism adaptation. *Percept Psychophys* 25:126–132
- Winer BJ (1971) *Statistical principles in experimental design*. McGraw-Hill, New York