Exp Brain Res (1999) 124:503–512

RESEARCH ARTICLE

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# Remembered positions: stored locations or stored postures?

Received: 24 September 1997 / Accepted: 11 August 1998

**Abstract** Many recent studies indicate that memory for final position is superior to memory for movement. There is ambiguity about what is meant by the term final position, however. Is it final spatial location or final posture? According to a recently proposed theory by Rosenbaum et al., which maintains that stored postures form the basis for movement planning, when people try to return to recently reached positions, they should try to adopt the postures they just occupied. An alternative view, which holds that movements are primarily planned with respect to spatial locations, predicts that subjects should tend to return to places in external space. We describe an experiment that tested these opposing predictions. The experiment relied on the notion that if people store and use postures, they should "copy" the posture adopted with one arm to the other arm when possible. The results support this hypothesis.

**Key words** Reaching movements · Memory for positions · Laterality · Posture copying · Human

## Introduction

When one reaches to a final position, what does one later remember – the movement, the final location, the final posture, or some combination of these elements? Although information in the literature bears indirectly on this question, we have been unable to find a direct answer to it in previously published research.

In this article, we review previous work that bears on the question of what is learned when people move repeatedly to a given position. Then we present two theoretical perspectives which make diverging predictions about what should be learned in repositioning tasks. One perspective predicts that final positions are remembered as postures; the other predicts that final positions are remembered as locations. We describe an experiment designed to distinguish between these two predictions. The experiment indicates that final postures are remembered and are "copied" from one arm to the other when subjects try to reach repeatedly to the same location in the midsagittal plane with alternating arms or when subjects try to reach repeatedly to the same location anywhere in the workspace with the same arm. In the last section of the article, we discuss the implications of our findings.

## Previous research on memory for position

A number of studies have shown that memory for final position is better than memory for movement. In one of the first such studies (Marteniuk and Roy 1972) subjects moved the hand to a stop and the experimenter then returned the subject's hand either to the original or to a different starting position. Next, subjects were asked to reproduce the distance they just covered. They did very badly when they had to reproduce the distance from a new starting position but they did well when they had to reproduce the distance from the original starting position. In another condition subjects again moved the hand to a stop and had the hand returned either to the same start position or to a different starting position; this time they were asked to bring the hand back to the final position they just reached. Surprisingly, they did well in this task, regardless of whether the starting position was the same as in the beginning. In fact, subjects managed to reach the final position even if the hand was moved passively back and forth during the initial movement. Results like these have been obtained in many studies (Kelso and Holt 1980; Jaric et al. 1992, 1994; Laabs 1973). See Smyth (1984) for an excellent review.

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The fact that final-position reproduction is better than distance reproduction has been taken to support the equilibrium-point hypothesis of motor control (Feldman 1966; Kelso and Holt 1980; Latash 1993), which emphasizes the establishment of target states for the neuromuscular system. One way of redescribing the superiority of final-position reproduction over distance reproduction in terms compatible with the equilibrium-point hypothesis is that actors remember final equilibrium states but do not remember means of reaching those equilibrium states. This redescription is supported by the observation that there is usually greater movement variability than terminal-position variability in targeted movements (Bootsma and Van Wieringen 1990; Desmurget et al. 1995; Wiesendanger et al. 1996).

## Defining “final position”

What is meant by the term “final position”? The term could mean the final location in external space to which a critical point along the limb segment chain (e.g., the tip of the index finger) is brought, or a final body state – for example, a vector of joint angles or, considering the dynamics as well as the kinematics of movement, a vector of muscle stiffnesses. As far as we know, no one has attempted to distinguish between the final-location and final-body-state interpretations.

## Final location

Which class of interpretation is correct? According to a classical view, originating with Tolman (1948), one would expect location to be the critical control parameter for position reproduction. Tolman showed that organisms learn the spatial layouts in which they move rather than the movements they make. Thus, a rat will get to the feeding area of a maze more quickly than in its first exposure to the maze even if its limbs are suddenly weighed down, if the maze is suddenly flooded, or if its starting place in the maze is altered. The rat has evidently learned the spatial layout of the maze, not the movements needed to traverse it.

The same general conclusion has been reached by other investigators working on manual control. In the case of manual reaction time tasks, the classical view of stimulus-response (S-R) compatibility effects is that S-R compatibility depends more on the location in external space where responses are made than on which hand makes the response (Brebner et al. 1972; Wallace 1971). Thus, pressing a key on the left in response to a stimulus on the left is easier than pressing a key on the left in response to a stimulus on the right, regardless of whether the key is pressed with the left hand or right.

A similar conclusion was reached by Wickens (1938), whose subjects participated in a shock-avoidance study. Extension of the finger enabled the subject to bring the finger away from the shock after a warning tone sounded. After training, the subject’s hand was inverted, so flexion rather than extension of the finger allowed the finger to escape the shock. Subjects immediately flexed the finger rather than extending it after the inversion, suggesting that they had not just learned movements.

A number of investigators have likewise proposed that movements are primarily planned in external spatial coordinates. A well-known hypothesis favoring spatial control of movement is the minimum-jerk hypothesis of Flash and Hogan (1985), according to which hand movements are typically designed to follow straight lines in extrinsic space. Flash and Hogan proposed more specifically that the kinematics of the end-effector (e.g., the tip of a hand-held stylus) generally respects a spatiotemporal pattern that permits minimization of the mean squared jerk (the third time derivative of position) of the end-effector in external space. Georgopoulos and his colleagues (e.g., Georgopoulos et al. 1981) have likewise suggested that the primate motor cortex primarily controls the spatial properties of arm trajectories. Insofar as both of these views are correct – something that is questionable, as seen below – they fit with the view that learned final positions are learned final locations.

## Final body states

Because controlling movements entails generation of appropriate muscle torques, lower-level details of movements must ultimately be taken into account for movements to achieve spatial goals. A growing body of evidence supports the view that movement planning is also based on these lower-level variables. With respect to Flash and Hogan’s (1985) minimum-jerk hypothesis, it has been shown that departures from straight-line motions in external space occur when loads are applied to the hand (Uno et al. 1989). Moreover, changes in movement curvature associated with different spatial directions can be ascribed to minimization of mean muscle tension change (Dornay et al. 1996). Although it has been suggested that directionally dependent departures from linearity may be due to visual misperception (Wolpert et al. 1994, 1995), this hypothesis has been rejected (Osu et al. 1997).

With respect to the hypothesis by Georgopoulos et al. (1981) that the primate motor cortex codes spatial properties of movement, recent studies have shown that discharge properties of motor cortex neurons depend on starting and ending arm postures for the same spatial displacements of the end-effector (Scott and Kalaska 1997). Hence, it can no longer be accepted that only spatial features of movement are represented in primate motor cortex, although it is possible that spatial features alone are represented elsewhere and that spatial features alone are represented in areas of primate motor cortex that have not yet been studied.

Findings such as these imply that body states are taken into account in motor control. However, they do not imply that spatial properties of movements are not taken into account. Everyday experience suggests that spatial properties must be provided for in some tasks (e.g., drawing a straight line). What is needed, then, is interactive control across different levels. Recent data concerning the kinematics of joint-angle changes for targeted hand movements (Haggard et al. 1995) indicate that spatial as well as kinesthetic constraints do indeed affect movement generation. Moreover, two recent models of the motor control system have emphasized cooperative consideration of constraints at many levels. Kawato (1996) developed a neural network model for bidirectional communication between higher and lower levels. D.A. Rosenbaum, R.G. Meulenbroek, C. Jansen, J. Vaughan (1998, unpublished) developed a cognitive psychological model with a hierarchy of constraints that can be adjusted according to task demands. In the theory of Rosenbaum et al. it is assumed that target locations are generally planned at a higher level than final postures, and that final postures are generally planned at a higher level than movements; see also Rosenbaum et al. (1993, 1995, unpublished) and Vaughan et al. (1997). The theory leaves open the possibility that final locations or final postures can be remembered since both elements are assumed to play a role in motor planning. However, because the theory assumes that movements are planned by making use of previously stored final postures, it would be favorable to the theory to show that final postures are remembered.

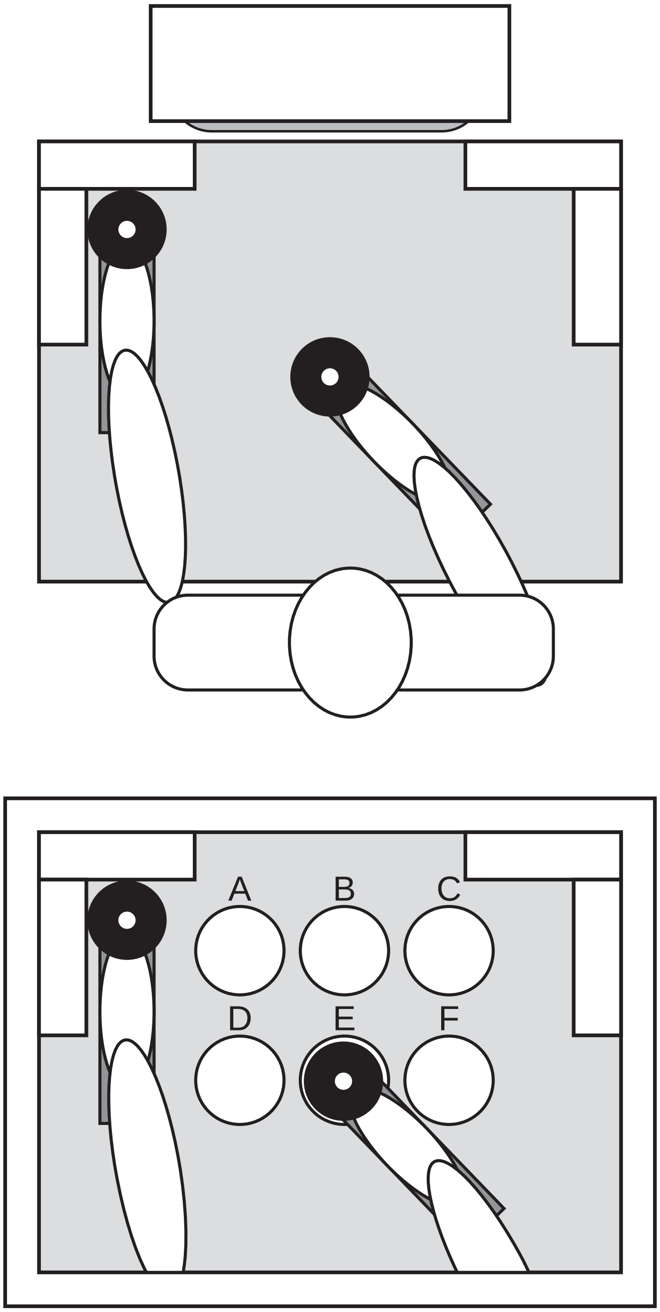

**Fig. 1** Setup for the experiment. *Top panel* Schematic view of the subject as seen from above. The subject faced a video monitor, shown opposite the subject's side of the table. Not shown is the video camera, mounted above the center of the table and pointed straight down. *Bottom panel* Schematic of the image seen by the subject on the video monitor. Neither diagram is drawn exactly to scale. The left hand is shown here in the resting position

## Experiment overview and predictions

In the present experiment, the subject sat at a table raised to chest height and began each experimental trial with the arms outstretched, resting on the table, and bent slightly at the elbows, as shown in Fig. 1. The task was to move either the left or right hand to a target and then to return the hand to its rest position. In the control conditions, the subject was supposed to move one hand – either the left or right – to the same target 20 times in a row, returning to the rest position between each reach. In the experimental conditions, the subject was also supposed to reach the same target 20 times in a row but to do so with alternating hands, again returning to the rest position between each reach. In both the control and experimental conditions, the first ten trials were performed with visual feedback and the final ten trials were performed without visual feedback. The targets were either in the body midline or to the left or right of the body midline. The targets in the body midline could be reached with symmetric arm postures; the targets off the body midline could not.

The main question concerned the way positions were remembered in those conditions where, a priori, the positions could be remembered either as postures or as locations – namely, midline targets reached for with alternating hands or with just one hand, and peripheral targets reached for with just one hand.

Four sets of predictions were tested. The first set concerned distances between successively adopted positions. If subjects remember postures when it makes sense to do so, distances between successively adopted positions should be lower in the conditions where only one hand is used than in the conditions where alternating hands are used. By contrast, if subjects only remember locations, distances between successively adopted positions should be no different in the one- and two-hand conditions. Admittedly, the former, posture-based, prediction is not very strong. Smaller within- than between-hand distances could be obtained for reasons other than posture storage. For example, there might be a tendency to play out the same motor commands repeatedly for the same hand, or there could be similar proprioceptive biases for the same hand. Nonetheless, it was important to test this prediction because its disconfirmation would vitiate the posture-store hypothesis.

A second set of predictions concerned distances between positions adopted in lag-2 rather than lag-1 (consecutive) reaches. Because all lag-2 distances were produced by one hand, either separated by a response made with that same hand (in the control condition), or by a response made with the other hand (in the experimental condition), different predictions could be made about lag-2 distances based on the location and posture hypotheses. If only locations are remembered, lag-2 distances should be the same in the control and experimental conditions – that is, regardless of whether the intervening response is made with the other hand or with the same hand. However, if postures are remembered, lag-2 distances should, in general, be smaller in the experimental (alternating-hand) condition than in the control (repeating-hand) condition because errors should accumulate as more and more responses are made with the same hand (Bock and Eckmiller 1986). The only way that the lag-2 distances could be the same in the control and experimental conditions, according to the posture hypothesis, is if posture copying from one arm to the other were perfect.

An elaboration of the prediction introduced in the last paragraph concerns the difference between lag-2 distances in the control and experimental conditions for midline versus non-midline targets. If postures adopted by one arm are "copied" to the other arm when it makes sense to do so (i.e., for midline targets reached for with alternating hands), then the difference between control- and experimental-condition lag-2 distances should be different for midline and non-midline targets. The basis for this prediction is that if the arm whose positions contribute to the lag-2 distance measure is affected (midline targets) or unaffected (non-midline targets) by the activity of the other arm between its first and second reaches, the difference between lag-2 distances in the control and experimental conditions should be different when posture copying either occurs (midline targets) or does not occur (non-midline targets).

A third set of predictions concerned correlations between positions adopted successively by the two hands when they moved in alternation to the same targets. According to the posture hypothesis, there should be stronger positive correlations in the in-out (*y*) direction for midline targets than for peripheral targets, and stronger negative correlations in the horizontal (*x*) direction for midline targets than for peripheral targets. By contrast, if only locations are stored, positive correlations should be observed between positions adopted by the two alternating hands both in the horizontal (*x*) and in the in-out (*y*) direction, and there should be no difference between positive correlations for midline versus peripheral targets. The latter, location-based predictions are based on the idea that if locations are remembered in a single coherent map, the hand used to get to a location should not matter. The former, posture-based, predictions are based on the idea that when subjects can copy postures from one arm to the other (i.e., for midline targets), one arm should approximately mirror what the other arm just did.

A fourth set of predictions provides a check on the third. Correlations between successively adopted positions might turn out as predicted by the posture hypothesis because each arm on its own might change where it ends up over successive positioning trials. Thus, if each arm exhibits the same cumulative bias to move in or out, the two arms moving in alternation could yield a positive correlation in the in-out direction, and this positive correlation could, conceivably, be more pronounced for midline targets than for peripheral targets. Similarly, if each arm exhibits the same cumulative bias to move eccentrically or medially, the two arms moving in alternation could yield a negative correlation in the horizontal direction, and this negative correlation could, conceivably, be more pronounced for midline targets than for peripheral targets. To check these possibilities, a further prediction of the posture-store hypothesis concerns the effects of interleaving target positions adopted by the two hands when only the left hand or right hand was used. If subjects copy postures from one arm to the other when they alternate between the two arms to reach medial targets, the obtained correlations should be weaker for interleaved hands than for alternating hands in the case of the medial targets. For peripheral targets, there should be no such weakening of interleaved-hands correlations compared to alternating-hands correlations because posture copying would not be expected for peripheral targets. Finally, if subjects return to previously reached locations but not to previously reached postures, no difference would be expected between interleaved-hands and alternating-hands correlations for any target.

## Materials and methods

Subjects made successive hand movements in the horizontal plane to each of six targets. Within each block of trials, subjects were supposed to reach to just one target, which was shown at the start of the block, either with one hand or with two hands in alternation. Each trial block began with vision (trials 1–10) followed by no vision (trials 11–20). The movements always began from fixed starting positions: The left hand extended out and to the left so that a manipulandum held with the left hand rested against an L-shaped frame mounted to the far left corner of the table top, as shown in Fig. 1. Similarly, the right hand extended out and to the right so a manipulandum held with the right hand rested against an L-shaped frame mounted to the far right corner of the table top. The target locations lay between the two arms, and were closer to the frontal plane of the body. In the control condition movements were made with just one hand (either the left or the right) in the entire series of 20 reaches for a given target, but in the experimental conditions the movements were made by alternating between the two hands (left, right, left, right ... or right, left, right, left, ...) to the same target 20 times in a row.

The subject sat at a table, which was raised to chest height, and moved the upper arm and forearm via shoulder and elbow rotations, respectively; the wrist could not bend. The subject's forearm and hand rested on a light wooden board with felt on its underside and two bands across the top for securing the forearm. With this arrangement, the subject could slide the board with very little friction over the table. The board for each arm was 55 cm long, 9 cm wide, and 1.5 cm thick and was equipped with a micro-switch resting beneath the tip of the index finger. When the subject pressed the switch, it illuminated a penlight mounted in the center of a thin wooden circular disk, 13 cm in diameter, positioned 2 cm over the hand, centered above the micro-switch. A small battery resting on the board sat just beyond the micro-switch and provided the power source for the light.

Over the table and pointing down toward it was a video camera which sent images of the workspace to a video monitor located beyond the table top, directly in front of the subject. On the video monitor, the subject could see his or her own movements during the opening trials of each experimental block. Movements away from the frontal plane of the body appeared as upward displacements on the video screen, movements toward the frontal plane of the body appeared as downward displacements, and movements to the right or left appeared as right or left displacements, respectively. A clear plastic sheet was superimposed on the video screen to indicate target positions. Six circles appeared on the sheet. Each circle had a unique letter: A, B, and C for the top left, top middle, and top right positions, respectively, and D, E, and F for the bottom left, bottom middle, and bottom right positions, respectively. The letters appeared above the circles. The circles were 10 cm in diameter. The image of the hand-driven disk was 8 cm in diameter. The target circles were positioned so the six possible positions of the disks filled as much of the workspace as possible and so each hand could reach comfortably to each position. Because each target circle's position was defined by just two spatial coordinates and only the shoulder and elbow could rotate, any given placement of the hand-driven circle in a spatial target required a unique posture.

At the start of each block of trials the experimenter announced which circle was the target for that block, whether one or two hands should be used to bring the moved circle into the target circle, and, in the event that two hands would be used, which hand was supposed to go first. The subject's task in each trial was to bring the designated hand circle to the designated target circle, hold the hand circle at rest until the subject judged it to coincide spatially with the circle on the screen, and then to switch on the light with the index finger of the positioned hand. Between trials, the subject had to keep both hands at the far corners of the table. L-shaped wooden frames were mounted on the table's far corners so the round disk above the hand could be pushed against the interior of the frame with the subject's arm outstretched. The subject could bring the manipulandum to the rest position by feel alone.

The same target was supposed to be reached 20 times in a row within each block of trials. The first ten reaches were completed with visual feedback. These trials allowed the subject to learn the target position for that block. After the tenth reach, once the hand was returned to the holding position, the experimenter flipped an opaque screen, attached to welder's goggles worn by the subject, down over the subject's eyes. The subject then continued the placement task for another ten trials. The experimenter indicated when the subject could stop the placements. Thus, the subject was not responsible for keeping track of the number of positioning trials.

While the task was being performed, the experimenter checked that the subject activated the light when reaching the judged position, that the correct hand was used in each trial, and that both hands were at their resting positions between trials. The entire session was videotaped, allowing for a later check that all aspects of the procedure were followed in all trials.

The experimental design called for two same-hand conditions and two alternating-hand conditions. One same-hand condition required the use of the left hand only (condition LL). The other same-hand condition required the use of the right hand only (condition RR). One alternating-hand condition began with the left hand (condition LR). The other alternating-hand condition began with the right hand (condition RL). The order of conditions was balanced so all four movement conditions were tested equally often in all serial positions, and such that all six targets were reached equally often in each movement condition and equally often in each serial position.

Nine Penn State undergraduates, four male and five female, served as subjects. All subjects were told to be as accurate as possible in all conditions and that a monetary bonus of U.S. $20 would be awarded to the subject whose accuracy was best. Each subject's session lasted about 50 min.

The data were analyzed using a video-digitizing technique developed by Barnes et al. (1989), which allows for recording the Cartesian coordinates of points of interest in video still frames. As shown by Fischer et al. (1994), interrater reliability with this method exceeds 0.98 and the standard error of discrepancies between mean positions digitized from video frames and mean positions for the same points measured directly with a ruler is less than 1 mm. In the present application, the operator saw the superimposed freeze-frame video and computer image and used the mouse to click on the position of the light bulb at the first video frame in which it was illuminated. This was done for all no-vision trials. The coder watched the initial ten trials of each block to make sure subjects complied with the instruction to bring the moved circle into the target circle when visual feedback was available.

## Results

Inspection of the videotape revealed that the basic procedure was followed by all subjects in all trials. During the vision-present trials, the moved circle was always brought within the target circle and the light was clicked on while the circle occupied that region. Furthermore, the subjects always brought both arms up against the L's at the far corners of the table between trials.

A summary of the results (Fig. 2) shows the first position adopted after the removal of visual feedback (trial 11) and the position adopted in the last no-vision trial (trial 20) both in the unimanual and bimanual conditions. Because there was no indication of a difference in performance in conditions LR or RL, those conditions have been combined.

As seen in Fig. 2, there were large shifts in adopted positions from the first to the last no-vision trials. In both of the one-hand conditions (LL and RR), adopted positions for targets farthest from the subject (top points in the left and right panels of Fig. 2) were generally farther from the subject in trial 20 than in trial 11, whereas for targets closer to the subject (bottom points in the left and right panels of Fig. 2) the adopted positions were generally closer to the subject in trial 20 than in trial 11 (except for the rightmost target in the left-hand case). In the alternating-hands conditions, the most striking feature of the results was the overall symmetry of the shifts: The inner (bottom) points were "attracted" toward the body center, and the outer (top) points were "attracted" to the centers of the distal portion of each arm's workspace.

### Distances between successive positions

As stated earlier, the first prediction of the posture-based model was that distances between positions adopted in successive trials (herewith, lag-1 distances) would be larger in the between-hand conditions than in the within-hand

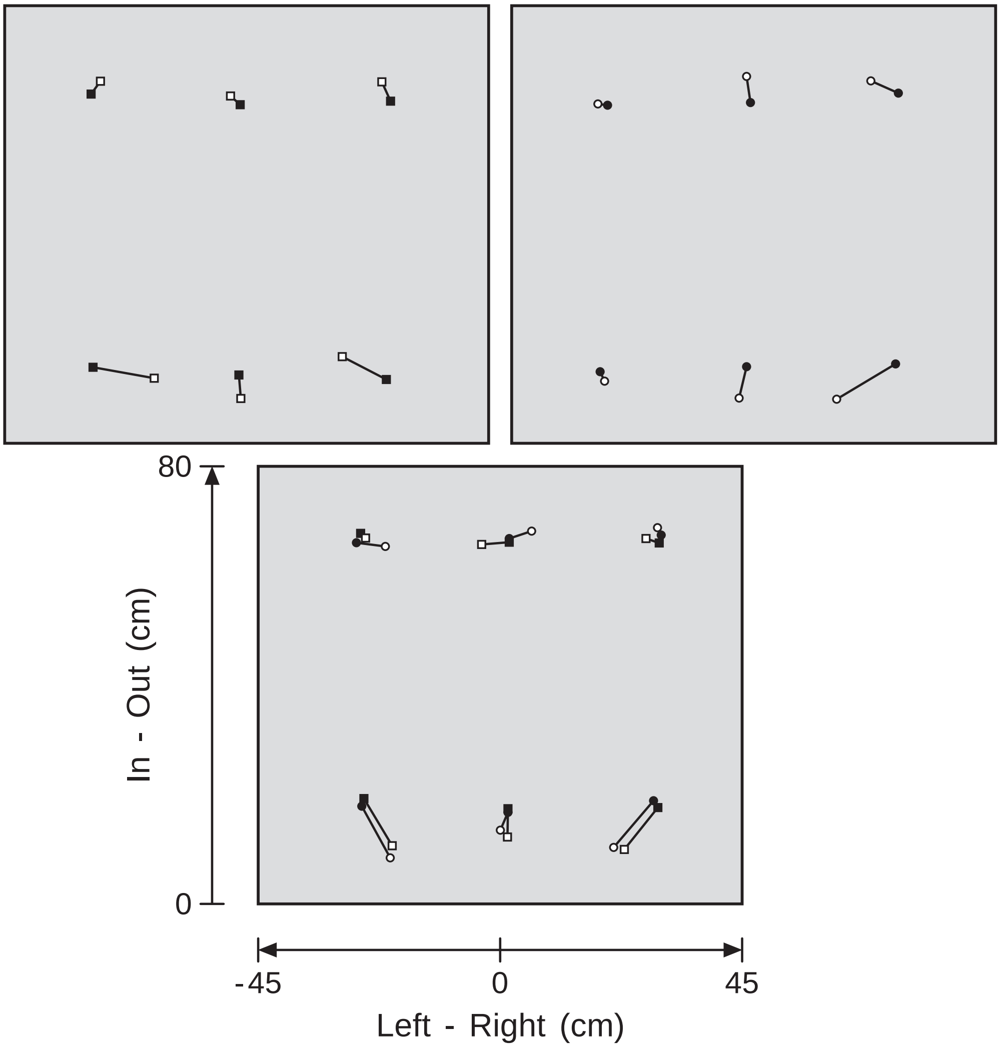

**Fig. 2** Mean positions adopted in condition LL (*top left panel*), condition RR (*top right panel*), and conditions LR and RL (*bottom panel*). *Solid points* represent positions in the first no-vision trial (trial 11). *Empty points* represent positions in the last no-vision trial (trial 20). *Circles* represent right-hand responses. *Squares* represent left-hand responses. Dimensions and lengths indicated for the bottom panel also apply to the top panels

**Table 1** Lag-1 distances (cm)[a]

| Condition | Target A | Target B | Target C | Target D | Target E | Target F |
|---|---|---|---|---|---|---|
| LL | 2.32 | 2.39 | 2.36 | 2.49 | 2.14 | 2.77 |
| RR | 2.10 | 2.39 | 2.10 | 2.94 | 2.14 | 2.25 |
| LR or RL | 4.08 | 5.85 | 4.88 | 5.72 | 4.33 | 5.29 |

[a] Data from no-vision trials only

**Table 2** Lag-2 distances (cm)[a]

| Condition | Target A | Target B | Target C | Target D | Target E | Target F |
|---|---|---|---|---|---|---|
| LL | 2.65 | 2.87 | 2.82 | 3.07 | 2.32 | 3.20 |
| RR | 2.65 | 2.85 | 2.46 | 3.48 | 2.39 | 2.90 |
| LR or RL | 2.10 | 2.27 | 2.69 | 3.48 | 2.12 | 2.79 |

[a] Data from no-vision trials only

conditions. As seen in Table 1, this prediction was confirmed. For every target, the lag-1 distance was greater in the between-hand condition than in the within-hand condition. These data were evaluated with a three-way analysis of variance (ANOVA) that tested the effects of the in-out (near-far) position of the target, the horizontal (left, middle, or right) position of the target, and response condition (LL, RR, or LR and RL combined). The effect of response condition was highly significant, $F(2, 16)=65.80$, $P<0.001$, as was the interaction between the in-out and horizontal target positions $F(2, 16)=5.67$, $P<0.01$. For outer (farther) targets, lag-1 distances were larger for middle positions than for lateral positions, whereas for inner (closer) targets, lag-1 distances were smaller for middle positions than for lateral positions. No other interactions or main effects were statistically significant; all associated $P$ values exceeded 0.10.

Next consider the second set of predictions, which concerned lag-2 distances. The relevant data are summarized in Table 2 and were analyzed in the same way as the lag-

**Table 3** Correlations between successive left-right positions[a]

| Condition | Target A | Target B | Target C | Target D | Target E | Target F |
|---|---|---|---|---|---|---|
| LL | 0.230 | 0.341 | 0.328 | 0.561 | 0.314 | 0.533 |
| RR | 0.479 | 0.140 | 0.469 | 0.329 | 0.236 | 0.529 |
| LR or RL | –0.342 | –0.692 | –0.370 | –0.279 | –0.568 | –0.224 |

[a]Data from no-vision trials only

**Table 4** Correlations between successive in-out positions[a]

| Condition | Target A | Target B | Target C | Target D | Target E | Target F |
|---|---|---|---|---|---|---|
| LL | 0.409 | 0.467 | 0.258 | 0.351 | 0.264 | 0.403 |
| RR | 0.307 | 0.409 | 0.570 | 0.413 | 0.492 | 0.518 |
| LR or RL | –0.031 | 0.077 | –0.163 | 0.097 | 0.156 | 0.330 |

[a] Data from no-vision trials only

1 distances. An ANOVA tested the effects of the in-out (near-far) position of the target, the horizontal position (left, middle, or right) of the target, and response condition (LL, RR, or LR and RL combined). The ANOVA revealed a significant effect of response condition, *F*(2, 16) =5.643, *P*=0.014. The mean lag 2 distance was 2.82 cm in the left-hand-only condition (LL), 2.75 cm in the right-hand-only condition (RR), and 2.45 cm in the two-hand condition (LR or RL). A Newman-Keuls test showed that the lag-2 distance in the two-hand condition was significantly smaller (*P*<0.05) than the lag-2 distance in either one-hand condition, and the two one-hand conditions did not differ significantly (*P*>0.05). These results are consistent with the expectation that error would build up for a hand when that hand was used repeatedly, as predicted by the posture hypothesis. The fact that lag-2 distances were smaller in the experimental conditions than in the control conditions is inconsistent with the location hypothesis, which predicted no such effect.

With respect to the elaboration of the posture hypothesis as applied to the lag-2 distances, the data provide mixed support for the posture hypothesis. On the basis of the posture hypothesis, it was predicted that the difference between lag-2 distances in the experimental and control conditions would be unequal for midline and peripheral targets. Inspection of Table 2 shows that this prediction was only partially confirmed. The difference between lag-2 distances in the experimental and control conditions for target B, the far medial target, was 0.59 cm, the largest for any of the six targets. However, the difference between lag-2 distances for target E, the near medial target, was only 0.24 cm. The differences between lag-2 distances for targets A and D, the two left targets, were 0.55 cm and –0.20 cm, respectively, and the differences between the lag-2 distances for targets C and F, the two right targets, were –0.05 cm and 0.26 cm, respectively.

## Correlations between positions

The next set of tests concerned correlations between successively adopted positions. As seen in Table 3, correlations between successive left-right positions were negatively correlated in the between-hand conditions but were positively correlated in the within-hand conditions. An ANOVA showed that the effect of response condition on horizontal position correlations was highly significant, *F*(2, 16)=109.04, *P*<0.001, as was the effect of the horizontal position of the target, *F*(2, 16)=21.47, *P*<0.001, and the effect of the in-out position of the target, *F*(1, 8)=13.60, *P*<0.01. However, no other main effect or interaction was statistically significant (all *P*'s>0.20).

Because the posture hypothesis predicted negative correlations between successive left-right positions in the alternating hands condition (LR/RL), it was important to test whether the correlations were significantly negative. To do so, for each of the nine subjects we counted the number of targets for which a negative correlation was obtained between successive left-right positions in the alternating hands condition (LR/RL). Then we performed a one-tailed *t*-test to see whether the obtained sample mean was significantly greater than the number that would be expected by chance to have negative correlations (i.e., three targets). The obtained sample mean, 5.11, was significantly different from 3, *t*=4.64, *P*<0.001, *df*=8. This result, like the others reported so far in this section, supports the posture hypothesis. As would be expected if participants copied one arm's posture to the other arm, left-right errors were mirrored from one arm to the other.

Correlations between successive in-out (*y*) positions are summarized in Table 4, where it is seen that all the correlations, except for two, were positive. The only exceptions were at the far lateral positions in the between-hand condition. The correlations between successively clicked in-out positions were evaluated with an ANOVA which showed that the *y*-position correlations were significantly affected by response condition (LL vs RR vs LR/RL), *F*(2, 16)=21.81, *P*<0.001. The mean values for the three response conditions were 0.359 for condition LL, 0.452 for condition RR, and 0.077 for condition LR/RL. A Newman-Keuls test showed that condition LR/RL was significantly different (*P*<0.01) from conditions LL and RR, but conditions LL and RR were not significantly different from each other. No other main effect or interaction was statistically significant (all *P*'s>0.09). Because the posture hypothesis predicted positive correlations between successive in-out positions in the alternating hands condition (LR/RL), it was important to test whether the correlations were significantly positive. To do so, we tallied the number of targets for each subject that yielded

**Table 5** Alternating-hands and interleaved-hands correlations between successive left-right and in-out positions[a]

| Dimension | Target | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A | | B | | C | | D | | E | | F | |
| | Alternating | Interleaved | Alternating | Interleaved | Alternating | Interleaved | Alternating | Interleaved | Alternating | Interleaved | Alternating | Interleaved |
| Left–right | −0.342 | −0.010 | −0.692 | 0.070 | −0.370 | 0.068 | −0.279 | 0.058 | −0.568 | 0.065 | −0.224 | 0.204 |
| In–out | −0.031 | 0.118 | 0.077 | 0.099 | −0.163 | 0.004 | 0.097 | 0.021 | 0.156 | 0.065 | 0.330 | 0.009 |

[a] Data from no-vision trials only

positive correlations and compared the obtained sample mean (3.11) to the mean expected by chance alone (3). Not surprisingly, the null hypothesis could not be rejected, $t$=0.286, $P$>0.39, $df$=8.

The final set of analyses concerned the fourth set of predictions, which pertained to the effects of interleaving positions adopted by each arm when only one arm was used in a block of trials. Recall that the question was whether the correlations between successively adopted positions by the two alternating hands would also be obtained if we interleaved the positions of the two hands when they performed the targeting tasks by themselves in separate blocks. The posture hypothesis, or more specifically the hypothesis that postures are copied from one arm to the other for midline targets, predicted that the correlations would be more pronounced for the alternating-hands correlations than for the interleaved-hands correlations in the case of midline targets, but that the correlations would be no more pronounced for the alternating-hands correlations than for the interleaved-hands correlations in the case of peripheral targets.

The data concerning interleaved and alternating hands correlations appear in Table 5. Consider first the left-right dimension. The main effect of data source (alternating-hands versus interleaved-hands) was highly significant, $F$(1, 8)=119.98, $P$<0.001, with the correlations from the alternating-hands source being significantly more pronounced (mean correlation=–0.412) than the correlations from the interleaved-hands source (mean correlation =0.076). The effect of target was also significant, $F$(5, 40)=2.91, $P$<0.03. Pairwise comparisons of alternating hands versus interleaved hands for individual targets, using the Newman-Keuls procedure, showed that only the two midline targets yielded significant differences between alternating-hands and interleaved-hands sources; both midline targets had $P$ values less than 0.01 for the source (alternating versus interleaved) effect. None of the peripheral targets had a significant pairwise difference between the two sources; the $P$ values for each of the four peripheral targets exceeded 0.05.

The in-out dimension failed to yield any effect of data source. Regardless of whether data came from alternating or interleaved hands, the mean correlation in successive in-out positions was slightly positive (0.077 for alternating hands vs 0.052 for interleaved hands), and no main effect or interaction involving data source approached statistical significance; all associated $P$ values exceeded 0.35.

## Discussion

The present experiment was designed to reveal how positions that can be remembered as locations or as postures are actually remembered. To address this question, we had subjects move to initially seen and then merely remembered positions, performing the task either with one hand or with two hands in alternation. We generated four sets of predictions to distinguish the location and posture hypotheses; all of the predictions concerned performance in the final ten trials of each block, when the positioning task was performed without benefit of vision. The results corresponding to the four sets of predictions generally supported the posture hypothesis. First, distances between successively adopted hand placements (lag-1 distances) were smaller in the one-hand conditions than in the two-hand conditions, consistent with the view that final postures, rather than only final locations, influenced position reproduction. This effect was different for middle and for lateral positions, as would be expected if the lag-1 distances depended on the utility of copying postures between arms. The fact that the difference was reversed for near and far targets is something that we cannot yet explain. Second, distances between positions adopted in non-consecutive reaches (lag-2 distances) were smaller in the alternating-hands and in the one-hand conditions, again as would be expected if aspects of subjects' postures affected position reproduction. The difference between lag-2 distances for the alternating-hands and one-hand conditions was largest for the far midline target, which was one of the two targets that could be reached with symmetric postures. Third, correlations between horizontal positions adopted by the two alternating hands were negative, most strongly so for the midline targets. This outcome is consistent with the view that subjects mirrored with one hand what they did with the other hand. Correlations between in-out positions adopted by the two alternating hands were often positive, as predicted by the posture hypothesis, but were not reliably positive over subjects; what this means will be discussed in the next paragraph. Fourth and finally, using interleaved horizontal positions from each of the hands when those hands were used individually yielded less pronounced negative correlations than using positions adopted by the two hands when those hands were used in regular alternation. This result indicates that the negative correlations for horizontal position in the alternating-hands conditions reflected mirroring of one hand's position by the other hand rather than an artifact of each hand's bias. There was no difference between interleaved- and alternating-hands correlations in the in-out dimension, however.

All in all, the results supported the hypothesis that positions that could be stored as postures were stored as such. The only result which failed to support this hypothesis was that correlations involving lag-1 and lag-2 positions in the in-out direction were not always reliable. Because the focus on left-right and in-out dimensions was somewhat arbitrary, however, being motivated principally by reliance on Cartesian coordinates for purposes of data analysis, the absence of reliable in-out correlations need not be taken as strong evidence against the posture hypothesis. What is more important is that the presence of reliable correlations for the left-right dimension is sufficient, along with the other results, to support the conclusion that subjects remembered postures and copied postures from one arm to the other when it made sense to do so.

The finding that there is posture-copying is reminiscent of the well-known fact that there are interactions between the two hands during bimanual performance (Swinnen et al. 1994). However, those interactions occur while the two hands move simultaneously. The new finding here is that interactions between the hands occur even when there is a considerable delay (about 1 s) between the two hands' motions. A future parametric study could vary the delay between successive hand movements to determine how long the delay must be for posture-copying to persist. It is interesting that in cyclic movements of the two hands, one hand slightly leads the other (Stucci and Viviani 1993; Swinnen et al. 1996; Treffner and Turvey 1995), as if information for one hand is passed immediately to the other hand. Our data suggest that this transfer occurs even when the other hand is not required to move immediately. In addition, the transferred information appears to persist for a relatively long time.

A final comment about our results concerns the implication of our findings for the classical view of learning mentioned at the outset of this article. According to this view, which originated with Tolman (1948), what is learned in spatial performance are spatial locations, not body positions. Our results do not show that final locations cannot be learned; indeed, final locations may have been learned here when the hands reached in alternation to peripheral targets. The fact that postures were apparently learned as well fits with the posture-based theory of motor planning developed by Rosenbaum et al. (1993, 1995, 1998) and helps explain the original results of Marteniuk and Roy (1972) – that when distances must be reproduced from original starting positions, performance is good, whereas when distances must be reproduced from different starting positions, performance is poor. When distances must be reproduced from original starting positions, the same final posture can be adopted in the induction and testing phases. However, when distances must be reproduced from different starting positions, the same final posture cannot be adopted in the induction and testing phases. The fact that performance was better when the same final posture could be adopted fits with the view that final postures are stored and relied on in the planning of movement.

**Acknowledgements** This study was supported by NSF grant SBR-94-96290, NIH Research Scientist Development Award KO2 MH00977, and a grant from the Research and Graduate Studies Office of Penn State University. Jason Bloom and Stephanie Lee helped with apparatus construction, data acquisition, and data analysis. Cathleen Moore and two anonymous reviewers provided helpful comments.

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