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End posture selection in manual positioning: evidence for feedforward modeling based on a movement choice method

Received: 2 April 2003 / Accepted: 6 May 2003 / Published online: 25 July 2003
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Abstract Although it is well known that the postures adopted at the ends of movements depend on where one starts and how one moves, it is not yet clear whether those differing end postures are selected before movements begin. Two experiments were designed to test the hypothesis that end postures for positioning movements are chosen before movements commence. The experiments were further designed to check whether movements are internally simulated before overt movements occur and end-postures are still being selected. To address these questions we used a *movement choice* method. Participants were presented with two possible end postures and were asked to choose between them by moving to the one that seemed easier to adopt. End-posture choices were affected by starting positions and also by the movements that would have to be made, as affected by having obstacles in the way. The results suggest that participants relied on feedforward modeling of prospective movements as they selected end postures prior to overt movement production. The fact that the movement choice method could confirm this suggests that the method holds considerable promise as a tool for investigating motor planning.

Keywords Cost containment · Feedforward modeling · Movement planning · Obstacle avoidance · Posture-based model

Introduction

A major goal of research on the planning of movements is to understand how particular movements are adopted

when more than one movement allows a task to be achieved. An emerging view is that the motor planning system relies on cost containment. The idea is that costs may either be minimized (Flash and Hogan 1985; Harris and Wolpert 1998; Nelson 1983; Uno et al. 1989) or kept below critical values (Rosenbaum et al. 2001a). Early models of cost containment focused on minimization of single costs such as jerk (Flash and Hogan 1985) or torque change (Uno et al. 1989). More recent models allow for minimization of multiple costs (Kawato 1996) or keeping multiple costs below critical values (Meulenbroek et al. 2001a, 2001b; Rosenbaum et al. 1995, 2001a, 2001b; Vaughan et al. 1998, 2001). According to the latter model, actors plan movements—or more specifically positioning movements of the hand—by evaluating possible end postures and movements to those end postures. The evaluation is done with respect to a number of constraints occupying a *constraint hierarchy* (i.e., a set of task-defined, rank-ordered requirements). For manual positioning tasks, a typical constraint hierarchy includes such factors as how close the hand should be to the target at the time of movement completion, how far the hand or arm should be from an obstacle, and how costly it should be to move from the starting posture to the end posture. In the model of Rosenbaum et al. candidate end postures and candidate movements are first evaluated with respect to the most important requirement in the constraint hierarchy, then with respect to the second-most-important requirement in the constraint hierarchy, and so on. The combination of end posture and movement that is finally selected satisfies the most requirements.

The idea that end postures are represented separately from movements was defended in several articles (Fischer et al. 1997; Meulenbroek et al. 1993; Rosenbaum et al. 1995, 2001a). Computer simulations showed that by combining this idea with the constraint hierarchy construct it is possible to generate realistic hand and arm movements for aiming (Rosenbaum et al. 1995), reaches around obstacles (Rosenbaum et al. 2001a; Vaughan et al. 2001), grasping (Meulenbroek et al. 2001a, 2001b; Rosenbaum et al. 2001a), and handwriting (Meulenbroek

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et al. 1996; Rosenbaum et al. 1995). Behavioral experiments also showed that detailed kinematics of reaching and grasping can be well fitted with the model (Meulenbroek et al. 2001a, 2001b; Rosenbaum et al. 2001b; Vaughan et al. 2001).

An assumption of the posture-based model of Rosenbaum et al. that has not yet been tested is that one criterion used for selecting end postures is how easy it is to reach those end postures from starting postures. In the model the ease of reaching an end posture from a starting posture is captured by the end posture's *travel cost*. The travel cost of an end posture depends on the sum of the angular distances that would have to be covered by the joints to bring the body from its starting posture to the chosen end posture. The angular displacements of the joints are weighted by their respective *expense factors*, which are assumed, for convenience, to remain fixed except when the health of the joints changes.

Are initial postures actually taken into account during end posture selection? Surprisingly, there is little direct evidence on this question. There is evidence that initial postures play a role in the way movements unfold, but this evidence does not strictly imply that final postures are specified before movements begin. It could also be taken to suggest that final postures are specified while movements are under way.

The evidence that initial postures play a role in the way movements unfold is as follows. First, people make more accurate rapid aiming movements if they can see the hand at its start position than if they cannot (Prablanc et al. 1979; Roy and Marteniuk 1974). Second, discharge properties of motor cortex neurons prior to arm movements depend on the arm's initial position (Kalaska et al. 1990; Scott and Kalaska 1997). Third, postures adopted at the ends of manual positioning movements depend on the postures from which the movements began (Buneo et al. 1997; Desmurget et al. 1998; Fischer et al. 1997; Soechting et al. 1995).

As mentioned above, it does not necessarily follow from these results that end-positions are specified *prior* to movement initiation. Indeed, some investigators have expressed doubt that initial postures do play a role in end-posture selection. Two of the most influential ideas in motor-control research are, in fact, founded on this idea. According to the equilibrium point (EP) hypothesis (Bizzi et al. 1992; Feldman 1986; Latash 1993), there is no reason to take initial positions into account, at least for simple joint rotations. Similarly, according to Donders' Law (for review, see Gallistel 1999; Gielen et al. 1997) the eye's torsion angle at the end of a gaze shift does not depend on the torsion angle from which the gaze shift begins. Gielen et al. (1997) have suggested that Donders' Law may also apply to arm movements (but see Buneo et al. 1997).

How can one determine whether end-positions are specified prior to movement? Here we introduce a new procedure, which may in fact be used to address other questions of interest in the study of action planning, as discussed later in this article. The procedure relies on

preferences. Participants are given a choice of two options. The question is which option they prefer. By studying preferences over a range of choice options one can infer the criterion or criteria participants use in their decision-making.

In the two experiments reported here we used this simple *movement choice* method to determine whether participants' end-position preferences would depend on their start positions. To anticipate the main result both experiments showed that end-position preferences depended on start positions. Experiment 2 also showed that participants take into account the movement paths that they would take to the possible end-positions.

Experiment 1

Method

In Experiment 1 participants chose between two end-positions, each of which was associated with a unique posture. Each choice was made from each of a number of starting positions. By varying the starting postures we could determine whether the choice of end posture depended on the initial posture.

Participants

Ten neurologically normal, right-handed Penn State students (five men, five women) participated in exchange for course credit. All participants were experimentally naive as to the purpose of the study. All participants signed an informed consent form before the experiment began and were tested in accordance with ethical guidelines established by, and explicitly approved for this experiment by, the Penn State University Institutional Review Board.

Materials

An OPTOTRAK motion recording system (Northern Digital, Waterloo, Ontario, Canada) was used to record the position of the arm and hand during the experiment. Infrared-emitting diodes (IREDs) were attached to the two shoulders, right elbow, right wrist, right thenar eminence, tip of the right thumb, and tip of the right index finger. In addition to the 11 IREDs just referred to, 4 additional IREDs were affixed to the top corners of a wooden block measuring 4×7.5×15 cm and weighing 0.17 kg. One of the long narrow sides of the block lay on the table surface and had felt attached to it to reduce friction. Participants slid this block of wood across the table surface. The OPTOTRAK was used to record the arm, hand, and block positions. A computer monitor in front of the participant displayed a rectangle corresponding to the position of the top surface of the hand-held block as well as rectangles corresponding to the home and two possible choice positions for each trial (Fig. 1). Participants wore a long-sleeve Lycra-Spandex shirt to reduce friction between the arm and table. This type of shirt lightly hugs the body in such a way that IREDs affixed to it faithfully represent the position of the body without constraining normal motion.

Procedure and design

Participants sat at a table that slanted down at a slight angle (15°). Participants were asked to lean the sternum against the close edge of the table, thus reducing extraneous movement of the torso. The slight incline of the table made it possible to maximize the visibility of the IREDs by the OPTOTRAK. Pilot work showed that the slight

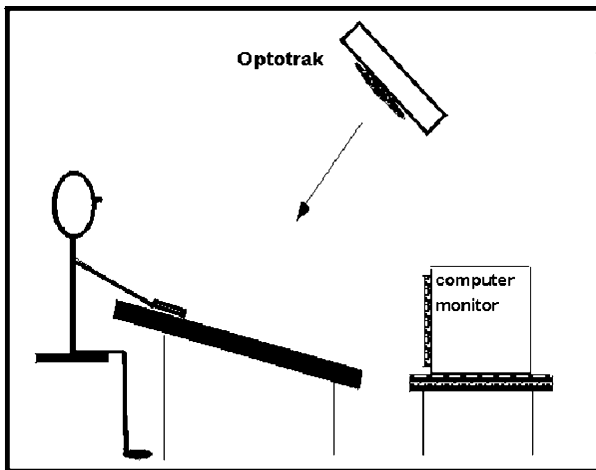


Fig. 1 Experimental set-up

incline of the table also allowed participants to perform longer without fatigue than when they moved the arm in a horizontal plane. The incline of the table enhanced participants' ability to maintain continual elbow, forearm, hand and block contact with the table.

Participants were asked to slide the wooden block along the table surface with the right hand, keeping the fingers in fixed positions around the sides of the block and keeping the arm, hand, and block on the table surface at all times. Participants looked at the computer monitor, which rested on a platform on the opposite side of the inclined table. The monitor showed a blue rectangle (0.5×2.5 cm) whose position corresponded to the current position of the top surface of the hand-held block. When the participant moved the block, its image moved in corresponding fashion on the computer display. The delay between block movement and image movement was imperceptible, and the mapping of actual movements to displayed movements was very easy to learn. After about 10–20 s of informal practice at the start of the session participants adapted to the system. All participants confirmed that the look and feel of the set-up was similar to using a computer mouse, something with which all the participants had a great deal of experience.

In each trial participants moved the blue rectangle into a stationary red rectangle that was slightly larger (1×3 cm) than the moved rectangle. The stationary red rectangle signaled the start position that the participant had to adopt. After the moved rectangle remained within the start-position rectangle for 500 ms, two other rectangles appeared and remained on the screen until the moved rectangle was brought into one of them. These rectangles were green and were the same size (1×3 cm) as the start rectangle. The instruction to the participant was simply to “move to one target or the other, whichever is easier.” There was no speed pressure.

The start and choice positions are shown in Fig. 2. There were eight start positions shown in the upper region of the display and three target positions shown in the lower region of the display (near body center). The x and y screen coordinates (in centimeters) for the centers of the four start circles were as follows: start 1 (82.7, 47.9), start 2 (117.6, 83.0), start 3 (187.8, 100.6), and start 4 (222.9, 66.3). The x and y screen coordinates (in centimeters) for the center of the choice circle were (152.8, 30.5). Each start position was tested with each of the three possible target choice pairs (AB, AC, and BC). The 8×3=24 choice conditions were tested in random order in each of ten blocks per participant.

Start and target positions were defined separately for each participant by determining the range of motion that the participant could achieve when the block was held in such a way that it occupied each of the circles shown in Fig. 2 and subject to the constraint that the elbow, forearm, hand, and block all remained in constant contact with the table. The procedure for determining the range of motion for each circle was as follows. The participant was

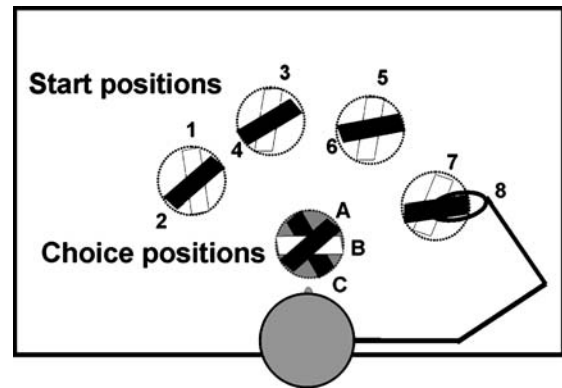


Fig. 2 Start positions (*numbers*) and choice positions (*letters*) for Experiment 1. Start circles are shown in white, and the choice circle is shown in gray. Circles used for defining start positions are visible here as dotted lines; they were not present during the experiment

asked to move the image of the hand-held block into a shown circle and then to rotate the hand as far as possible in the counterclockwise direction while keeping the image of the rectangle in the circle. Next, the participant was asked to rotate the hand as far as possible in the clockwise direction while keeping the image of the rectangle in the circle. These two extreme positions defined the range of joint angles for that circle. This process was repeated for each of the four start circles and also for the circle at the center of the workspace, which was where the choices were made. The three choice options defined in the circle at body center corresponded to the extreme positions that could be adopted within the circle, as well as the position halfway between these extremes. The experimenter was present at all times to monitor performance.

Results

Choice probabilities

The probability of choosing one position rather than another was calculated for each choice position both as a function of start position and as a function of choice alternative (Fig. 3). To evaluate these factors statistically one analysis of variance focused on the likelihood of choosing option A when the alternative was B or when the alternative was C, and this factor was crossed with the eight start positions. A second analysis of variance focused on the likelihood of choosing B when the alternative was A or C, again crossed with the eight start positions. A third analysis of variance focused on the likelihood of choosing C when the alternative was A or B, once again crossed with the eight start positions. These three ANOVAs were not independent, but including all of them allowed us to develop a clear picture of the factors leading to the selection of a given choice position.

For target choice A there was a significant main effect of start position, $F(7,63)=2.96$, $P\leq 0.01$, as well as a significant main effect of alternative choice position (B as opposed to C), $F(1,9)=9.96$, $P\leq 0.01$. The interaction between start position and alternative choice was not significant, $F(7,63)=0.39$, n.s. These results show that participants were more likely to choose position A when

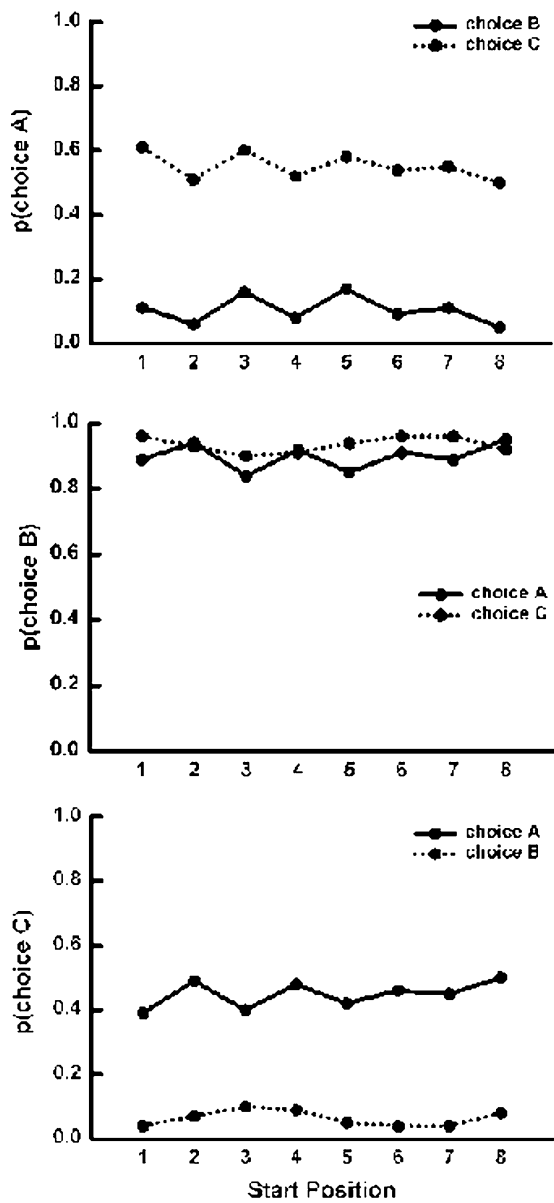


Fig. 3 Probability of choosing end-position A (*top panel*), end-position B (*center panel*), and end-position C (*lower panel*) given the two alternative end-positions and eight start positions

the start positions required wrist angles that matched the wrist angle adopted for A (i.e., start positions 1, 3, 5, 7) than when the start positions did not match A (i.e., start positions 2, 4, 6, 8).

For target choice B there was a significant main effect of start position, $F(7,63)=2.90$, $P\leq 0.01$, but no main effect of alternative choice, $F(1,9)=0.72$, n.s., nor a significant interaction between start position and alternative choice, $F(7,63)=1.30$, n.s. The likelihood of choosing B increased as one started from positions to the far left or right, and decreased when the start positions were closer to body center.

For target choice C there was no main effect of start position, $F(7,63)=1.25$, n.s., but there was a main effect of

alternative choice, $F(1,9)=7.37$, $P\leq 0.05$, and a significant interaction between start position and alternative choice $F(7,63)=2.0$, $P\leq 0.05$. The probability of choosing C increased when the start wrist positions approximated the wrist position that could be adopted at C (start positions 2, 4, 6, and 8).

Model fitting

The results just presented suggest that there was an effect of start position, which supports the predictions of the posture-based model. Another way to evaluate the model is to see how well it fits the choice data when its goodness of fit is compared with the goodness of fit achieved with a model that has the same number of free parameters but does not assume consideration of start positions. For ease of exposition, we refer to the latter, alternative, model as the *end-only* model. We refer to the posture-based model in this context as the *start-and-end* model.

To fit the start-and-end (posture-based) model to the data, we relied on the fact that this model says that start postures are taken into account in selecting end postures by considering the travel costs of the joints. The travel costs are defined by the angular distances the joints must cover weighted by their respective expense factors. The model could be fitted to the choice data by parametrically varying the expense factors of the shoulder, elbow, and wrist until the sum of squared deviations between the observed and predicted choice probabilities was minimized.

To compute the squared deviations we had to generate predicted choice probabilities. For this purpose we assumed that the likelihood, $p(A|B)$, of choosing end posture A given B (to use an arbitrary pair for illustration) depends on the ratio of their respective travel costs:

$$p(A|B) = 1 - \frac{TC_A}{TC_A + TC_B} \quad (1)$$

where TC_A and TC_B are the travel costs for A and B, respectively. The travel cost, TC, for any posture could be calculated by taking the sum of the angular distances for the j th joint between its start, s_j , and final, f_j positions, weighted by the joint's expense factor:

$$TC = \sum_{j=1}^3 \text{Expense}_j |f_j - s_j| \quad (2)$$

The best fitting expense factors were explored by taking 21 equally spaced angles from 0% to 100%, inclusive, of each joint's range of motion, resulting in $21^3=9,261$ combinations of expense factors for each end-posture choice given each start posture.

To fit the end-only model we assumed that there are preferred angles for the shoulder, elbow, and wrist and that the preferred position would be one that comes as close as possible to those preferred angles (Baud-Bovy and Viviani 1998; Cruse 1986). Fitting the model amounted to exploring different possible values for the

Table 1 Best fitting parameter values (P1, P2, P3) and proportion of variance accounted for (R^2) for the end-only model and start-and-end (posture-based) model applied to the observed choice probabilities in Experiment 1. For each model the R^2 values and best fitting parameter values are given for all ten subjects (S1–S10). P1, P2, and P3 denote best fitting parameter estimates for the preferred shoulder, preferred elbow, and preferred wrist, respectively, expressed as percentages of the joint range for the end-only model, and best fitting expense factors for the shoulder, elbow and wrist, respectively, expressed as a percentage of the range 0–100% for the start-and-end (posture-based) model

S	End only				Start and end			
	R^2	P1	P2	P3	R^2	P1	P2	P3
1	0.532	75	25	40	0.988	5	5	5
2	0.809	76	15	18	0.987	5	5	5
3	0.498	76	20	30	0.990	5	5	5
4	0.731	80	30	51	0.965	5	5	5
5	0.611	85	20	25	0.976	5	5	5
6	0.675	80	15	65	0.978	5	5	5
7	0.497	100	0	40	0.981	5	5	5
8	0.751	80	15	55	0.969	5	5	5
9	0.778	75	30	70	0.975	5	5	5
10	0.875	80	35	59	0.971	5	5	5

preferred shoulder, elbow and wrist (expressed as percentages of the joint angle ranges adopted for this task). The best fitting parameters were found by exploring 21 equally spaced intervals from 0% to 100%, inclusive, of the range adopted for each joint. A cost, EC, for ending at an end posture was calculated as the sum of the squared angular differences between each joint's final angle, f_j , and preferred angle, p_j :

$$EC = \sum_{j=1}^3 (f_j - p_j)^2 \quad (3)$$

The likelihood of choosing one end posture, A, over another end posture, B, was assumed to depend on the ratios of their costs:

$$p(A|B) = 1 - \frac{EC_A}{EC_A + EC_B} \quad (4)$$

The results of the model fitting appear in Table 1. The start-and-end model accounted for a mean of 98.3% of the variance in participants' choice data. By contrast, the end-only model accounted for a mean of only 67.7% of the variance. In addition, the best fitting cost assignments for the wrist, shoulder and elbow were homogeneous over participants for the start-and-end model but were heterogeneous over participants for the end-only model. Both models were sensitive to the values of their three parameters. In the case of the start-and-end (posture-based) model it was possible to account for as little as 29% of the variance with some parameter combinations; however, as stated above, the best fitting parameter combinations allowed for better than 98.3% of the variance. The fact that the start-and-end model could yield a low R^2 value indicates that the model was rejectable.

Discussion

Experiment 1 used the new movement-choice method to test the hypothesis that choice of end posture depends on starting posture. We asked participants to adopt several start positions that differed with respect to shoulder, elbow, and wrist angle, and then to choose between different pairs of end postures. We found robust start position effects for two of the three end choices (targets A and B). Our finding that start postures can affect end-posture choices is consistent with the predictions of the posture-based model.

In further support of the posture-based model we found that it accounted for more variance than did an alternative model which assigned priority to coming as close as possible to preferred joint angles regardless of which joints angles were adopted at the start. This alternative, end-only, model could be best fit to the choice data of the individual participants only when the preferred angles for the shoulder, elbow, and wrist varied considerably over participants. By contrast, the start-and-end (posture-based) model could be best fit to the choice data of the individual participants when the joints were assigned homogeneous (equal) expense factors over participants. The best fitting expense factors for the shoulder, elbow, and wrist were the same for all participants. This outcome was not an artifact of model insensitivity because there were combinations of expense factors for the shoulder, elbow, and wrist that led to worse fits than were achieved with the end-only model.

Experiment 2

In the second experiment we exploited the movement choice method to investigate an open question within the posture-based model. The question was whether end-posture choices depend on characteristics of the movements to be made from the start postures to the end posture. The first experiment provided evidence that travel costs play a role in end-posture choices. This outcome is broadly consistent with the view that anticipated movements play a role in end-posture selection. Still, the movements required in the first experiment were direct. That is, they could be achieved through simple interpolation between starting and ending postures. It is not clear, therefore, whether participants actually considered full movements between starting and ending postures in the choices they made. Another possibility is that they merely considered differences in angular positions between starting postures and candidate end postures and computed travel costs accordingly.

To evaluate the possibility that participants actually considered movements between starting and end postures in end-posture selection we asked in Experiment 2 how choices of end-position would be affected by having or not having an obstacle between the start and end-position. Because different movement paths were required to reach the end-position when an obstacle was present, finding an

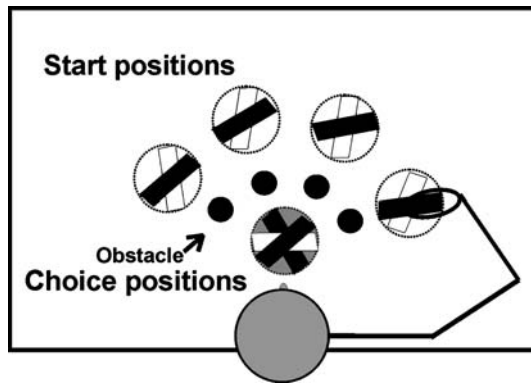


Fig. 4 Start positions, choice positions, and obstacle positions for Experiment 2. Start circles are shown in *white*, and the choice circle is shown in *gray*. Each start position had a unique obstacle—the *black circle* between it and the circle containing the choice positions

effect of obstacle presence on end-posture choice would accord with the hypothesis that movements per se are taken into account in end-posture selection.

Method

Participants

Ten neurologically normal, right-handed Penn State students (five men, five women) participated in exchange for course credit. All participants were naive to the purpose of the study. None had participated in Experiment 1. As in Experiment 1, all participants signed an informed consent form before the experiment began and were tested in accordance with ethical guidelines established by, and explicitly approved for this experiment by, the Penn State University Institutional Review Board.

Materials

The experimental set-up was analogous to that used in Experiment 1.

Procedure

Targets were defined using the same procedure as in Experiment 1. Participants performed the same task as in Experiment 1 except that on one-half the trials an obstacle appeared between the start and choice circle (Fig. 4). There were eight start positions that varied with respect to shoulder angle, elbow angle, and wrist angle, and three possible choice pairs that varied with respect to wrist angle, elbow angle, and shoulder angle. The obstacle was a circle (2.5 cm in diameter) that appeared at the same time as the two choice rectangles. The center of the obstacle was positioned at the midpoint between the center of the start position and the center of the choice positions. The screen coordinates for the start circles and choice circle were identical to those used in Experiment 1. The *x* and *y* coordinates (in centimeters) for the centers of the four obstacles were as follows: obstacle 1 (117.6, 39.1), obstacle 2 (135.2, 56.7), obstacle 3 (170.4, 65.5), and obstacle 4 (187.8, 47.9). Participants were instructed to avoid contact with the obstacle. If the hand-held block contacted the obstacle, a warning tone sounded. There were 48 conditions altogether, which were tested in random order in each of the ten blocks in which each subject participated. Start positions, end-positions, and movements were recorded for each trial.

Results

Participants were able to avoid the obstacle in every experimental trial. This outcome shows that participants attended carefully to the instructions and feedback they received.

Choice probabilities

The probability of choosing one position rather than another was calculated for each choice position as a function of start position and obstacle condition (Fig. 5). An analysis of variance was performed for each of the possible choice target probabilities to examine the effect of obstacle condition, start position, and other possible choice.

For target choice A there was a significant main effect of start position, $F(7,63)=3.60$, $P\leq 0.01$, and a significant main effect of alternative choice position, $F(1,9)=5.90$, $P\leq 0.05$. There was also a significant interaction between obstacle condition and start position, $F(7,63)=2.87$, $P\leq 0.01$. However, there was no main effect of obstacle condition, $F(1,9)=0.28$, *n.s.*, and no other interaction was significant. In the obstacle-absent condition, participants were more likely to choose target choice A when the wrist angle at the start position approximated the choice A wrist angle (start positions 1, 3, 5, 7) than when it did not. By contrast, in the obstacle-present condition participants were more likely to choose position A in the matching start positions and the nonmatching targets for start positions 5–8 (those start positions to the right of body center).

For target choice B there was a main effect of start position, $F(7,63)=2.12$, $P\leq 0.05$, and a significant interaction between start position and alternative choice, $F(7,63)=4.49$, $P\leq 0.001$, as well as a significant three-way interaction among obstacle condition, start position, and alternative choice, $F(7,63)=2.57$, $P\leq 0.05$. There was no main effect of obstacle condition, $F(1,9)=0.85$, *n.s.*, and no main effect of alternative choice, $F(1,9)=0.27$, *n.s.*, nor was there a significant interaction between obstacle condition and start position, $F(7,63)=1.24$, *n.s.*

For target choice C, there was a significant main effect of start position, $F(7,63)=3.47$, $P\leq 0.01$, and a significant interaction between obstacle condition and start position, $F(7,63)=3.77$, $P\leq 0.01$. Participants were more likely to select position C in the obstacle-present condition than in the obstacle-absent condition when the start positions were to the left of body center, but they were less likely to choose position C in the obstacle-present condition than in the obstacle-absent condition when the start positions were to the right of body center. There was no main effect of obstacle condition, $F(1,9)=0.83$, *n.s.*, and no main effect of alternative choice, $F(1,9)=2.86$, *n.s.*, nor was there a significant interaction between obstacle condition and alternative choice $F(1,9)=0.004$, *n.s.* There was no significant interaction between start position and alternative choice, $F(7,63)=1.98$, *n.s.*, and no significant inter-

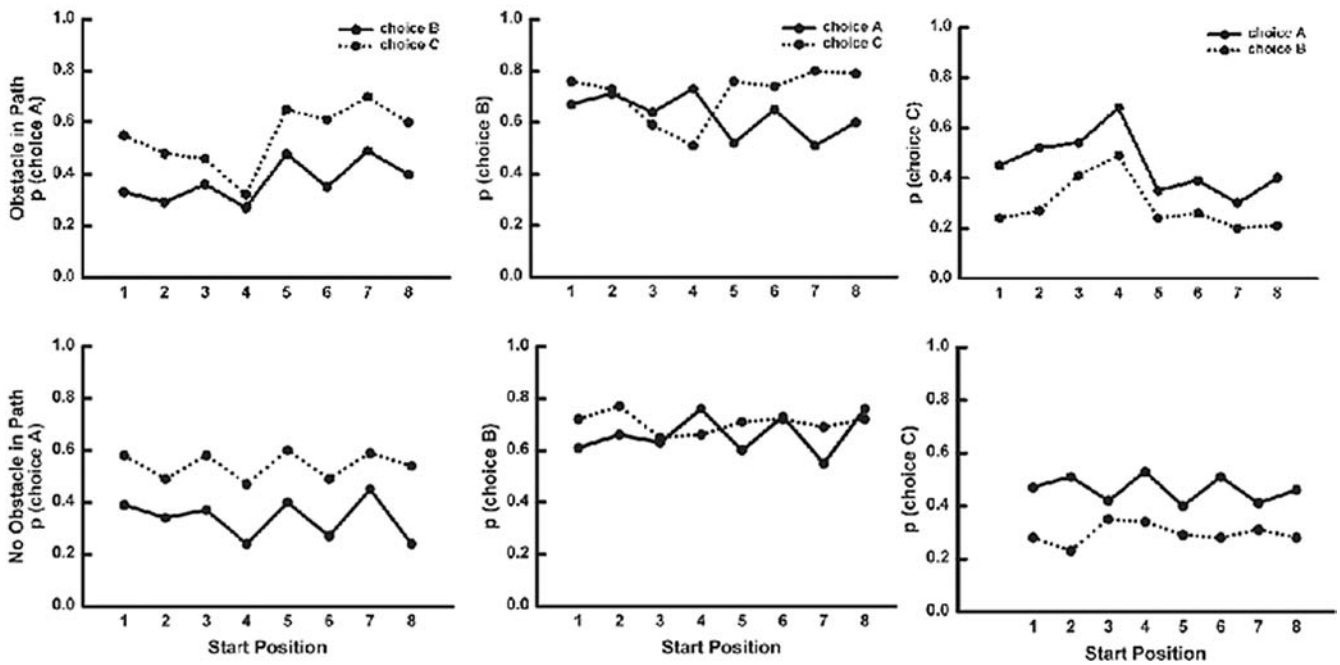


Fig. 5 Probability of choosing end-position A (left panel), end-position B (center panel), and end-position C (right panel) given the two alternative end-positions and eight start positions in the

obstacle-present condition (top row) and the obstacle-absent condition (bottom row)

action between obstacle condition, start position, and alternative choice, $F(7,63)=0.92$, n.s.

Model fitting

Model fitting for Experiment 2 was accomplished in the same way as in Experiment 1. The results appear in Table 2. As in Experiment 1, the start-and-end (posture-based) model accounted for more variance than did the end-only model. The start-and-end model accounted for an average of 98% of the variance, whereas the end-only model accounted for an average of only 48% of the variance. The best fitting expense factors for the shoulder, elbow, and wrist were homogeneous over participants for the start-and-end model. By contrast, the best fitting preferred angles for the shoulder, elbow, and wrist were heterogeneous over participants for the end-only model. It was possible to find parameter combinations for the start-and-end (posture-based) model that caused it to account for less variance than the end-only model, showing that it was possible to reject the start-and-end model in favor of the end-only-model.

Movement paths

Because a focus of the second experiment was the role of movement paths, we next evaluated the contribution of movement paths to end-posture choices. To characterize movement paths at a level of description appropriate to the question at hand we focused on a single measure: How

Table 2 Best fitting parameter values (P1, P2, P3) and proportion of variance accounted for (R^2) for the end-only model and start-and-end (posture-based) model applied to the observed choice probabilities in Experiment 2. For each model the r^2 values and best fitting parameter values are given for all ten subjects (S1–S10). P1, P2, and P3 denote best fitting parameter estimates for the preferred shoulder, preferred elbow, and preferred wrist, respectively, expressed as percentages of the joint range for the end-only model, and best fitting expense factors for the shoulder, elbow and wrist, respectively, expressed as a percentage of the range 0–100% for the start-and-end (posture-based) model

S	End only				Start and end			
	R^2	P1	P2	P3	R^2	P1	P2	P3
1	0.026	95	80	95	0.985	5	5	5
2	0.644	0	15	10	0.991	5	5	5
3	0.302	100	20	0	0.972	5	5	5
4	0.884	75	0	75	0.971	5	5	5
5	0.770	100	30	0	0.993	5	5	5
6	0.728	95	5	38	0.968	5	5	5
7	0.734	50	16	50	0.963	5	5	5
8	0.307	65	0	55	0.989	5	5	5
9	0.730	80	30	34	0.992	5	5	5
10	0.116	35	30	40	0.984	5	5	5

close was the manipulandum (the moved rectangle) to the obstacle when it was transported around it? We calculated the distance between the center of the obstacle and the center of the rectangle when it first passed from each start position through the vertical position (y value in Cartesian coordinates) corresponding to the center of the obstacle, regardless of whether the rectangle passed to the left or right of the obstacle. The first question was whether this horizontal position was different if an obstacle was

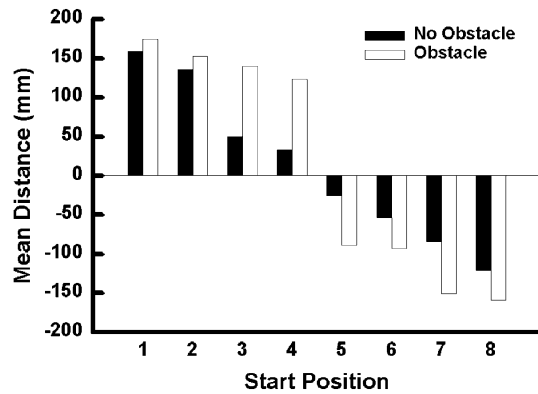


Fig. 6 Mean distance (mm) of the moved block from the center of the obstacle when its height corresponded to the obstacle center for that start position. *Positive values* indicate rightward distances. *Negative values* indicate leftward distances

present or not. The second question was whether, given a particular start position, the likelihood of choosing one end-position or another depended on this horizontal position.

Data relevant to the first question appear in Fig. 6. These data were evaluated with an analysis of variance which revealed a main effect of start position, $F(7,32)=1882.4$, $P \leq 0.0001$, a significant interaction between obstacle condition and start position, $F(7,32)=127.66$, $P \leq 0.0001$, but no main effect of obstacle presence or absence, $F(1,32)=0.07$, n.s. As seen in Fig. 6, horizontal positions were to the right of the obstacles for left starts (1–4) and to the left of the obstacle for right starts (5–8). These data show that movement paths between the start and end-positions were indeed affected by the presence of intervening obstacles.

The next, more important question was whether end posture choices were affected by the changes in movement path. The relevant data appear in Fig. 7. The independent variable in each of the three graphs is the difference, for each start position, between the horizontal position of the moved block in the obstacle-present and the obstacle-absent conditions (effectively, the difference in the heights of the black and white bars for each start position in Fig. 6). The top panel shows the difference in the likelihood, $p(A|A \text{ or } B)$, of choosing end-position A given the choice end-positions A or B in the obstacle-present and obstacle-absent condition. The middle panel shows the comparable difference for $p(A|A \text{ or } C)$. The bottom panel shows the comparable difference for $p(B|B \text{ or } C)$. Note that the difference in likelihood for $p(B|A \text{ or } B)$, for $p(C|A \text{ or } C)$, and for $p(C|B \text{ or } C)$ are redundant with the probability changes shown in Fig. 7, and therefore they are not shown.

As is apparent from Fig. 7, the likelihood of choosing a particular end-position changed with horizontal shifts in the movement paths. The likelihood of choosing A over B, A over C, and B over C all decreased as the horizontal position of the hand-held block shifted toward the right in the obstacle-present condition compared to the obstacle-

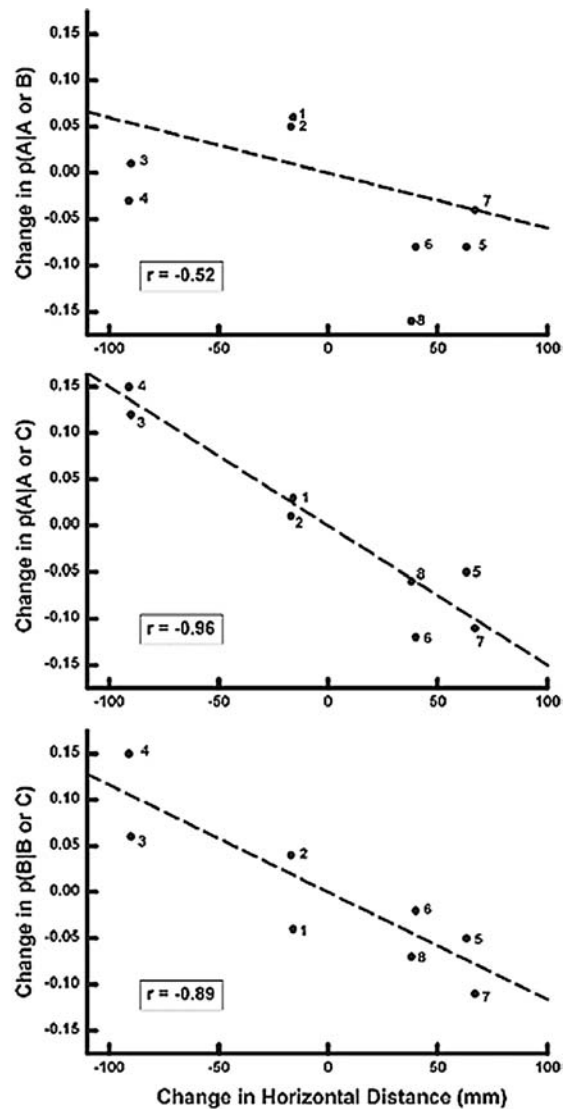


Fig. 7 Change in likelihood of choosing A over B (*top panel*), A over C (*middle panel*), and B over C (*bottom panel*) as a function of change in horizontal position of the moved-block center as it passed the height of the obstacle (i.e., difference between black and gray bar height for each start position in Fig. 6.) The *number beside each point* is the start position. The *dashed line* in each panel is the best fitting straight line for the linear function relating change in likelihood to change in horizontal position

absent condition. The strength of this relation was robust for the change in $p(A|A \text{ or } C)$, $t=7.901$, $P=0.0002$, and for the change in $p(B|B \text{ or } C)$, $t=4.70$, $P=0.0033$, but not for the change in $p(A|A \text{ or } B)$, $t=1.5$, $P=0.184$. The lack of significance of the latter result was not of special concern to us since our aim in this analysis was to see whether there was any effect of movement path on the likelihood of choosing an end posture. We found such an effect for $p(A|A \text{ or } C)$ and for $p(B|B \text{ or } C)$.

Discussion

The second experiment replicated the main finding of Experiment 1 that end-position choices were affected by start positions. The second experiment also provided data bearing on the question of whether choice of end postures takes required movement into account. To test this hypothesis we compared end-position choices for the same start and end-position possibilities when there was an obstacle in the path or when there was no obstacle in the path. We found that end-position choices were influenced by the presence of an obstacle in the movement path. This outcome is consistent with the hypothesis that participants considered the movements they could make to the end-positions under consideration. The outcome is also consistent with the account of obstacle avoidance provided by the posture-based motion planning theory (Rosenbaum et al. 2001a, 2001b). According to the theory, movements that permit obstacle avoidance are internally specified before the movements are performed and are linked to the specification of goal postures. Simulations of reaching around obstacles based on this idea are kinematically realistic, even at the level of individual rotations.

General discussion

This study addressed three main questions: (a) Are end postures selected prior to movement initiation rather than being mere consequences of movement? (b) If end postures are selected in advance, are they selected with respect to start postures? (c) Are forthcoming movements taken into account in the end-posture selection process?

To pursue these questions we used a movement choice procedure in which we relied on participants' preferences to infer the factors that participants take into account in motor planning. Our results showed that when participants chose between two presented end states, their choices depended on the travel costs associated with displacement from the current starting posture. In the second experiment we found that forthcoming movements to potential end postures affected end-posture choices. The latter conclusion is at odds with the view that participants only considered differences between starting postures and end postures in their end-posture choices.

Taken as a whole, the present findings dispel the concern that previously reported effects of starting positions on final adopted positions (Buneo et al. 1997; Fischer et al. 1997; Soechting et al. 1995) reflected retrospective rather than prospective control. That is, the data reported here suggest that end postures are planned prior to movement initiation (prospective control) and are not simply the emergent consequences of completed movements (retrospective control). If participants in the present study had relied on retrospective control, it is unlikely that we would have obtained reliable choice data, where end states were depicted in advance.

A question that arises about the interpretation given to our data is whether end postures were actually selected while movements were under way rather than before movements began. While we cannot rule out this possibility, several factors make us doubtful that this alternative explanation is correct. First, it is well known that early phases of movements predict their terminal properties. Thus, the initial speed of positioning movements is scaled to later peak speed, and peak speed is scaled in turn to movement amplitude (for review, see Rosenbaum et al. 2001a, 2001b). Second, the fact that movements tend to obey implicit constraints such as minimizing jerk or minimizing mean torque change also suggests that end states are represented in advance of movement initiation. This is because the computations required to optimize movements in these ways depend on information about final position and final time (again, for review, see Rosenbaum et al. 2001a, 2001b). Third, the time it takes to initiate movements has been shown to reflect advance knowledge of the final position that will be adopted. For example, the time to initiate a reach to an object differs if the object will be spontaneously grasped with one hand posture (an overhand grasp) or another (an underhand grasp) (Rosenbaum et al. 1992). Similar effects have also been reported by Brown et al. (2002). Fourth and finally, it has recently been shown that electrical stimulation of primary motor cortex and premotor cortex for extended durations (0.5 s) causes the unrestrained monkey to adopt characteristic postures regardless of its starting posture (Graziano et al. 2002). The latter result clearly indicates that there are neural circuits which can define terminal postures before movements begin.

The fact that potential movements affected our participants' choices, as shown in Experiment 2, suggests that the internal process of selecting end-positions includes a feedforward model of candidate movements. It is possible that in our experiments participants internally simulated the movements they could make and chose the one that seemed easier. If this method were used, the end posture would still have been represented in advance of overt movement initiation.

Inferring that our participants relied on internal simulations of possible movements is consistent with computational work on the importance of internal representations of body states with time-varying information for prediction and control (Wolpert and Ghahramani 2000). Recent functional imaging approaches to understanding the neural substrates of movement planning also support the idea that the brain (especially the parietal region) relies on kinesthetic models of movements (Rushworth et al. 1997, 2001; Sirigu et al. 1999; Wolpert et al. 1998). Studies of motor imagery lead to a similar conclusion (Jeannerod 1994a, 1994b; Johnson 1998, 2000; Parsons 1987; Sirigu et al. 1996, 1999).

How is it possible that end-positions are known before movements start but the nature of the movement to be performed affects end-position choices? There are two possibilities, both of which pertain to how participants

carry out internal simulations of possible forthcoming activity. One possibility is that they first identify end-positions and then compute the movement that will bridge the gap between the starting and end-positions. This is the method hypothesized in the posture-based model. Another possibility is that the internal simulations start with movements, where the movements are either determined randomly or through retrieval of previous movements for tasks similar to the current one, perhaps taking into account factors such as inertial sensitivity (Sabes and Jordan 1997; Sabes et al. 1998). At the ends of these internally simulated or recalled movements, anticipated end-positions would be cognitively available. We cannot distinguish between these theoretical possibilities at this stage of our research. However, we have offered arguments in other papers on the posture-based model for why we think end-positions are internally specified before movements are internally specified during the planning of forthcoming, overt movements. Further research is needed to distinguish between these two models.

Setting aside the question of how the foregoing two models can be distinguished, we wish to end this article by emphasizing more strongly than we have so far the possible value of the movement choice method. New methods help to advance knowledge. The method introduced here of asking participants to pick an action which they prefer out of a pair of alternatives has not been used before in motor control research, at least to our knowledge. As we have shown, parametrically varying features of the action choices can reveal the factors that participants take into account in the planning process. Clearly the movement choice method can be used in a wide range of circumstances. For example, the method can be used to determine the extent to which kinetic factors are taken into account in movement planning. In the present study we considered travel costs purely in kinematic terms. If loads were applied to the forearm so that different force profiles were associated with different candidate movements, participants' movement choices might pick up on this. For example, if people assign a premium to minimizing work (Buneo et al. 1997; Soechting et al. 1995), movements that are chosen should consistently entail less work than movements that are not chosen. Similar logic can be used to evaluate other hypotheses about the factors that are taken into account during the planning of motor acts.

Acknowledgements This article is based on a dissertation by the first author submitted in partial fulfillment of the requirements for the PhD degree at Pennsylvania State University. We thank Jeremy Graham for help with computer programming, Mark Latash and Cathleen Moore for helpful comments during the course of the research, and an anonymous reviewer as well as John Rothwell for helpful challenges in the revision process. This study was first described at the Second Annual Progress in Motor Control Conference, Pennsylvania State University, University Park, Pa., August, 1999. The research was supported by National Science Foundation Grant SBR-9496290, National Institutes of Health Grant 1 R15 NS41887-01, and a grant from the Research Graduate Studies Office of Pennsylvania State University.

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