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RESEARCH ARTICLES

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Posture-based or trajectory-based movement planning: a comparison of direct and indirect pointing movements

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Abstract Various models have been proposed in the literature to explain the control of human arm movements. To make a quantitative comparison between the predictions of various models, we tested subjects for movements to targets on a vertical screen in various conditions. Subjects were asked to move directly from one target to another, or to move by a via-point, at various movement velocities and in a condition with a weight of 0.6 kg attached to the forearm. This set of experimental data was used for comparison with the predictions by various posture-based and trajectory-based models on 3-D movement planning and control. Small but significant effects of starting position and path towards the target were found on the torsion of the arm at the end of the movement. No effects of movement velocity and weight attached to the forearm were found. The experimental results differed significantly from the predictions by any of the models considered. Of the models considered, Donders' law best predicts the experimental data. Our data indicate that future tests of models for motor control (1) should compare the predictions of not just one, but several models to a data set, and (2) should include not only planar, but rather 3-D movements in such a comparison.

Keywords Arm movements · Motor control · Movement planning · Pointing

Introduction

Various models have been proposed to explain the planning and execution of arm movements (Feldman and Levin 1995; Gielen et al. 1997; Harris and Wolpert 1998; Rosenbaum et al. 1995, 2001; Soechting et al. 1995; Uno et al. 1989). These models can be classified into two categories. The first category, which we will refer to as 'posture-based', assumes that a final posture is selected for each target position of the finger tip. Examples of models within the posture-based category are Donders' law (Von Helmholtz 1867) and the equilibrium point hypothesis (Feldman and Levin 1995). Donders' law predicts that the final posture does not depend on the initial posture. Models within the second category, which we will refer to as 'trajectory-based', use a criterion according to which an optimal trajectory towards the final finger position is selected based on the initial posture and the final finger position out of many possible trajectories. The final posture of the arm results from the selected trajectory. Examples of models within the trajectory-based category are the minimum work model (Soechting et al. 1995), the minimum torque-change model (Uno et al. 1989), and the minimum-variance model (Harris and Wolpert 1998). The knowledge model of Rosenbaum et al. (1995, 2001) is a special case within this classification scheme. In the knowledge model a final posture is selected before movement execution, which would make the model posture-based. However, this final posture is selected both on the basis of a spatial and a travel-cost criterion, making the model trajectory-based. This means that the model incorporates aspects of both planning strategies.

Several studies have tried to discriminate between models to account for observed movement data. Soechting et al. (1995) compared the predictions of Donders' law and the minimum work hypothesis with experimental data. In their study participants were instructed to point towards targets starting from different positions in 3-D space. An effect of starting position on the posture of the arm at the end of the pointing movement was found, which argues against Donders' law. Gielen et al. (1997) replicated this result. Additional evidence against Donders' law was found by Desmurget et al. (1998) who instructed participants to grasp a cylinder while initiating their movements from different starting postures. The initial posture at the beginning of the movement was found to affect the posture of the arm at the end of the movement.

An additional comparison between Donders' law and the minimum work hypothesis was performed by Vetter et

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al. (2002), who asked participants to touch a target bar using a handheld virtual stick. Predictions for the relative amounts of upper arm and forearm torsion of the two models were compared with the measured torsion. A small but significant violation of Donders' law was found. However, the data could not be explained by the minimum work model either, which predicted much larger effects of starting position on the final arm posture than observed.

In a series of experiments Desmurget and colleagues (Desmurget et al. 1995, 1998; Grea et al. 2000) tried to discriminate between posture-based and trajectory-based models by investigating the effect of a change in target position or target orientation at movement onset on the final arm posture. Desmurget et al. (1995) asked participants to grasp a bar. In a proportion of the trials the orientation of this bar was changed at movement onset. A similar task was used by Desmurget et al. (1998), who asked participants to grasp a bar from different initial positions. In this study the orientation of the bar could change at movement onset. Grea et al. (2000) asked participants to grasp a sphere. In some of the trials the position of the sphere changed at movement onset. By changing the target's position or the target's orientation at movement onset, the observed movement trajectories changed with respect to those in unperturbed movements. The targets' orientation or position before did not affect the posture of the arm at the end of the movement. This result argues in favor of posture-based models, like Donders' law. The study by Desmurget et al. (1998) also showed that the initial posture of the arm affected the posture of the arm at the end of the movement. This result argues against Donders' law.

The studies carried out up to now could not decisively discriminate between trajectory-based and posture-based planning, nor did they provide compelling evidence in favor of one of the specific models for movement execution, thereby rejecting others. Several studies presented evidence against Donders' law (Desmurget et al. 1998; Gielen et al. 1997; Soechting et al. 1995; Vetter et al. 2002) but other studies could not reject this law (Desmurget et al. 1995, 1998; Grea et al. 2000). The results by Vetter et al. (2002) present evidence against Donders' law, but the violations of this law are very small and could not be predicted by the minimum work model either. Moreover, few studies tested the minimum torque-change hypothesis extensively for movements in 3-D. However, there is good evidence that the minimum commanded-torque-change model or the angular-jerk model might provide better predictions of experimental data than the minimum torque-change model (Wada et al. 2001). Following our definition of posture-based and trajectory-based models, the best way to discriminate between posture-based and trajectory-based planning is to investigate the effect of the path towards the goal position on the final arm posture. Trajectory-based models predict that the final arm posture depends on the path, while posture-based models predict that the final arm posture is independent of the path. To our knowledge, this test and a quantitative comparison with predictions by various models for movements in 3-D has not been performed before.

In this study we tried to discriminate between various models (trajectory-based or posture-based) describing human arm movements by asking participants to make point-to-point arm movements to various targets in 3-D via different trajectories. In half of the trials participants were asked to move directly to a target, starting from various positions, while in the other half of the trials they were asked to move to the target position from the same starting positions by a so-called via-point. Donders' law was considered as the null-hypothesis that begin position and movement path do not affect final posture.

In general, arm movements are expected to be smooth, to require little energy, and to avoid extreme joint torques. Therefore, a detailed comparison of the predictions of the various models of motor control will be necessary to determine which, if any, criterion is used in human movement planning. For such a detailed comparison of the different models we added two additional conditions to our experiment. First, we varied the velocity at which participants were asked to move from one target to another, thereby trying to replicate the results of a study by Nishikawa et al. (1999). In their study no effect of movement velocity on final posture was found, which is consistent with predictions by the minimum work model and by Donders' law. An effect of movement velocity on the final posture would be consistent with predictions by the knowledge model, due to the optimal movement time included in the travel cost criterion used in the model (Rosenbaum et al. 1995). In addition to variations in the path towards the target position, in starting position, and in movement velocity, we attached a weight to the forearm of the participant in one of the conditions. The data of this condition were compared with the data without such a weight. The minimum work and the minimum torque-change model predict an effect of load on the final posture, whereas posture-based models such as Donders' law do not predict an effect.

Method

Participants

In each experimental condition ten participants took part. Nine participants took part in all conditions. One participant dropped out after the pointing task with and without a weight attached to the arm. Another participant replaced this subject for the fast and slow pointing movements tasks. The age of the participants ranged from 16 to 56 years (mean age of 31, standard deviation of 12.3). Two participants were left-handed. These left-handed participants were asked to perform the pointing movements with their right hand, like the other participants. On inspection of their movement data (average change in upper arm torsion, movements paths) no obvious differences were found with the data of the right-handed participants. Five participants, who were not members of the department, were paid for their participation. None of the participants had any known history of sensory or motor disorders. Before the start of the experiment subjects were informed about the experimental protocol, which was approved by the Medical Ethical Committee of the University of Nijmegen. All participants gave their informed consent for their participation in the experiment. The participation by the 16-year-old subject was approved by his parents.

Apparatus

During the pointing task participants were seated in a chair. A Philips 4750 LCD projector was used to project the stimuli on a 2.5×2 m vertical projection screen. Stimuli were presented within a 115×86 cm display image on the vertical screen. The presentation of the stimuli was controlled by a PC. During the experiment the orientation of the upper arm and the forearm of the participant was measured using two bracelets, each with 14 infra-red light-emitting diodes (IREDs). Ten of the IREDs were distributed equally across the bracelet in a zigzag pattern which consisted of two rings with five IREDs each with a distance of 4 cm between the two rings. The remaining four IREDS were attached to the edges of a cross of 5 cm in diameter attached to the bracelet. The location of the IREDs was recorded using an Optotrak 3020 system. The orientation and location of each bracelet was determined using the programs Rigmaker and Rigid provided with the Optotrak system. The orientation of each bracelet could be measured with an accuracy better than 0.5 deg. In one of the conditions a weight of 0.6 kg was attached symmetrically around the wrist of the participant, at a distance of about 28 cm from the elbow.

Stimuli

Stimuli consisted of red and green filled circles with a diameter of 6 cm projected on the projection screen by the LCD projector. Red circles represented final target locations. The green circles represented the via-points. The positions of the stimuli with respect to the participant are illustrated in Fig. 1. Each of the stimuli could serve as a target or a via-point. All stimuli were presented within a distance of 80 cm from the shoulder. Figure 1a shows a top view of the participant and the screen. Participants were facing the projection screen under an angle to allow them to point comfortably to the upper left stimulus. Figure 1b shows the positions of the stimuli on the screen. Using the Optotrak system, the locations of the stimuli were measured with respect to a coordinate system centered at the right shoulder. The horizontal axis of this coordinate system was chosen to pass through both shoulders. The other axes were orthogonal to the horizontal axis. One axis was oriented upwards and one straight forward relative to the subject. The center circle was presented at coordinates (51, −15, 17), where the first coordinate represents the depth, the second coordinate the horizontal distance, and the third coordinate the vertical distance. The upper left circle was presented at (63, 38, 30), the upper right circle coordinates were (39, −36, 29), and the bottom circle was presented at (52, −19, −11). All distances were measured in centimeters. Because most circles were presented closer to the shoulder than the length of the outstretched arm (the upper left circle could just be reached by the participants), participants bent their arms during their arm movements. At the end of each movement they touched the target with their finger.

The orientation of upper arm and forearm at each target was expressed as a rotation vector (in degrees) (Haslwanter 1995) from the mean posture adopted by the participant while pointing to the center target.

Design

Participants performed pointing movements in each of four conditions: (1) ‘no weight’ and without an instruction on movement speed; (2) ‘weight’, with a weight of 0.6 kg attached to the forearm, (no instruction of the movement speed); (3) ‘fast’, where participants were asked to move fast from target to target, resulting in an average movement time of 0.73 s (SD = 0.086 s); and (4) ‘slow’, in which participants were asked to move slowly from one target to the other, trying to arrive at the target location when the next target was presented, resulting in an average movement time of 1.3 s (SD = 0.18 s). In the ‘fast’ condition the inter-trial time was set to 1.5 s. In the ‘no weight’ and ‘weight’ conditions the inter-trial time was 2 s, while in the ‘slow’ condition an inter-trial time of 2.5 s was used.

The four conditions were presented in four separate blocks. The ‘no weight’ and the ‘weight’ conditions were presented in one session, and the ‘slow’ and ‘fast’ conditions were presented in another session. The order of the sessions and the order of the conditions within the sessions were randomized across participants. Within each condition eight blocks with 25 trials each were presented. At the first trial of each block the central target was presented. The posture of the arm when pointing to this target was used to determine the reference posture. The second trial moved the participant’s finger from the center target to one of the outer targets in a direct movement. The first two trials of each block were followed by a random sequence of direct and indirect movements. For each new trial the next target was selected at random. Also, direct and indirect movements were selected at random for each new trial.

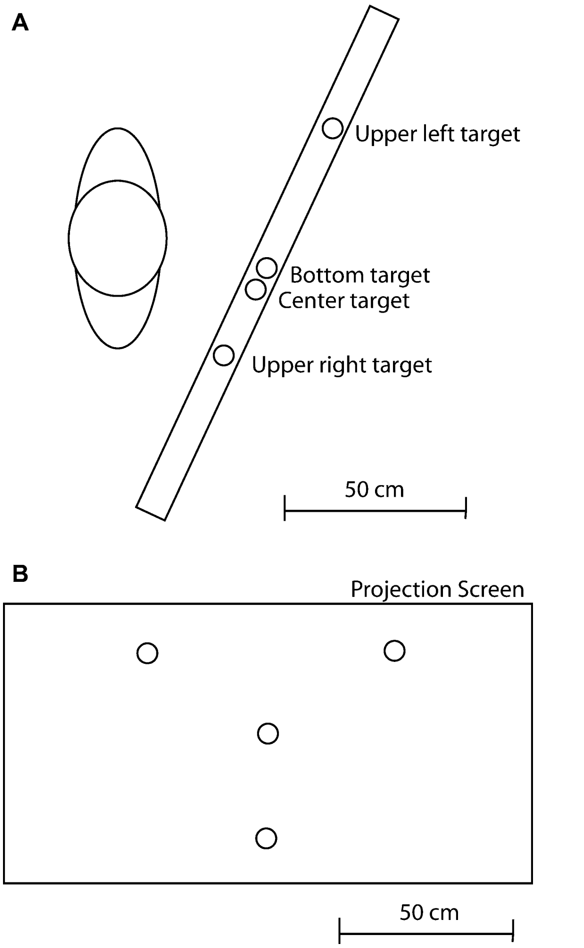


Fig. 1a, b The position of the stimuli in the experiment. The stimuli were projected on a projection screen which participants viewed under an angle (**a**). The projected stimuli were organized in a triangle with respect to each other, with the reference stimulus in the center (**b**)

Procedure

At the beginning of the experiment participants were seated in a chair. The right shoulder was fixated by means of a diagonal seat belt. Participants were told they would be presented with green and red circles on the projection screen. Their task was to point to the red target, moving their finger via the green target. They were asked to keep pointing to the red target until the next set of circles appeared on the screen accompanied by a computer beep. If the new green circle appeared at the location of the red circle of the previous trial (the new green circle then appeared under the finger tip of the participant), they were instructed to point to the red circle directly. To become acquainted with the task, participants received practice trials until they could carry out the task correctly.

Model simulations

In order to quantitatively compare experimental data and model predictions we simulated arm movements for three trajectory-based criteria: (1) the minimum work criterion; (2) the minimum angular jerk criterion; and (3) a minimum travel cost criterion. Moreover, the results were compared with predictions by Donders' law, which states that final posture does not depend on previous postures, on movement velocity, or on the load attached to the forearm. We did not simulate arm movements predicted by the minimum torque-change criterion, since convergence to the optimal movement trajectory was sometimes hard to obtain. In addition, Wada et al. (2001) showed that the minimum commanded torque-change model gave more accurate predictions than the minimum torque-change model and that minimum angular jerk simulations can be used as a good approximation to the predictions by the minimum commanded torque-change model. The amount of peak work, W, during an arm movement can be computed using the following equation:

$$\begin{aligned} W = \tfrac{1}{2}\Big(& I_1\left(\dot{\eta}^2\sin^2\theta + \dot{\theta}^2\right) + I_2\left(\dot{\eta}\cos\theta + \dot{\zeta}\right)^2 + \\ & I_3\left(\Omega_x^2 + \Omega_y^2\cos^2\phi + \Omega_z^2\sin^2\phi + \dot{\phi}^2 + 2\dot{\phi}\Omega_x\Omega_y\cos\phi\sin\phi\right) + \\ & I_4\left(\Omega_y^2\sin\phi^2 + \Omega_z^2\cos\phi^2 - 2\Omega_z\Omega_y\cos\phi\sin\phi\right) + \\ & 2A\left(\Omega_y^2\cos^2\phi + \Omega_x^2\cos\phi + \Omega_z\Omega_y\sin\phi + \dot{\phi}\Omega_x\cos\phi\right)\Big) \end{aligned} \tag{1}$$

Here φ represents the elbow flexion angle (φ=0 corresponding to full extension), η and θ represent the yaw and elevation angles at the shoulder respectively, and ζ represents the upper arm torsion. For a more detailed definition of these joint angles, of the inertia constants I_1, I_2, I_3, I_4, and the angular velocities Ω_x, Ω_y, Ω_z, see Soechting et al. (1995). Like Soechting et al., the optimal trajectory was selected as the trajectory with minimum work halfway through the trajectory.

The minimum angular jerk criterion (see Wada et al. 2001) minimizes the function:

$$C_{AJ} = \frac{1}{2}\int_0^{t_f}\sum_{i=1}^{4}\left(\frac{d^3\theta_i}{dt^3}\right)^2 dt \tag{2}$$

where the θ_i represent the joint angles (flexion/extension of the elbow, and three orthogonal rotation axes at the shoulder). The integration is over the time interval between movement onset (t=0) and movement offset ($t=t_f$). The path in joint space according to this criterion is a fifth order spline.

The minimum travel cost criterion is used in the model of Rosenbaum and colleagues (1995, 2001). The model assumes that the final posture of a movement is determined by comparing all postures stored in memory. The stored posture which best fits a set of constraints is selected. An important constraint is a small travel cost. After the best stored posture is selected, a grid search is performed around the stored posture until the end of the available planning time is reached. If the time to plan the movement is unrestricted, a grid search over the entire posture space is performed. In this case the optimal solution does not depend on the set of stored postures. To compare the predictions of the knowledge model with the predictions of the other models, we assume that postures are based on the low travel cost constraint only, and that planning time is unrestricted. With these assumptions the entire space of possible end postures is searched for the posture with the minimal travel cost. The travel cost is computed by the following equation:

$$V_p = \sum_{j=1}^{4}\left(\frac{k_j\alpha_j}{r}\left\{1 + \left[T_j - k_j\ln\left(\alpha_j + 1\right)\right]^2\right\}\right) \tag{3}$$

where the α_j denote the change in the joint angles of each of the four degrees of freedom (three in the shoulder, one in the elbow). The k_j's are constants related to the joint stiffness. We set these constants equal to 1 (Rosenbaum et al. 2001).

For each of the models (minimum work, minimum travel cost, minimum angular jerk) the minimum value of the cost function was found by a grid search. That is, we varied the torsion angle, ζ, from −180 to 180 deg in steps of 1 deg, and computed the other three angles (denoted η, θ, and φ using the fact that the finger is at the starting position and the target position at the begin and end of the movement, respectively), taking into account the normal physiological movement range of the joints. The elbow angle φ can be computed from the distance towards the target. The shoulder angles η and θ were found by means of a simplex search. For all values of the upper arm torsion, ζ, we determined the corresponding value of the cost function.

For the comparison of the data for the 'no weight' condition with the model predictions we used a movement duration of 1 s. For the starting posture of each simulated movement, we used the mean observed posture of the arm corresponding to that starting position.

Results

Figures 2 and 3 show the mean torsion of the upper arm and the forearm, respectively, at the three targets without instructions regarding movement speed ('no weight') and with a weight attached to the subject's wrist ('weight'). Torsion was defined as the angle of rotation along the longer axis of the upper arm or forearm with respect to the average orientation while pointing to the center target. Bars indicate the mean torsion across subjects. Lines on top of the bars represent the 95% confidence intervals across participants.

A repeated measures analysis of variance tested the effects of starting position, weight attached to the forearm, and path (direct movement or a movement along a via-point) for each of the three targets. This analysis provides a direct test of Donders' law, since the law predicts no effects of starting position, path towards the goal position, and the weight attached to the forearm on the final posture of the arm.

Small, but significant effects were found of the path towards the target position and of starting position on both forearm and upper arm torsion for all three targets. The size of these effects was typically a few degrees. No significant effects were found of the weight attached to the forearm.

Specifically, for the bottom target a significant interaction effect was found of path and starting position on the

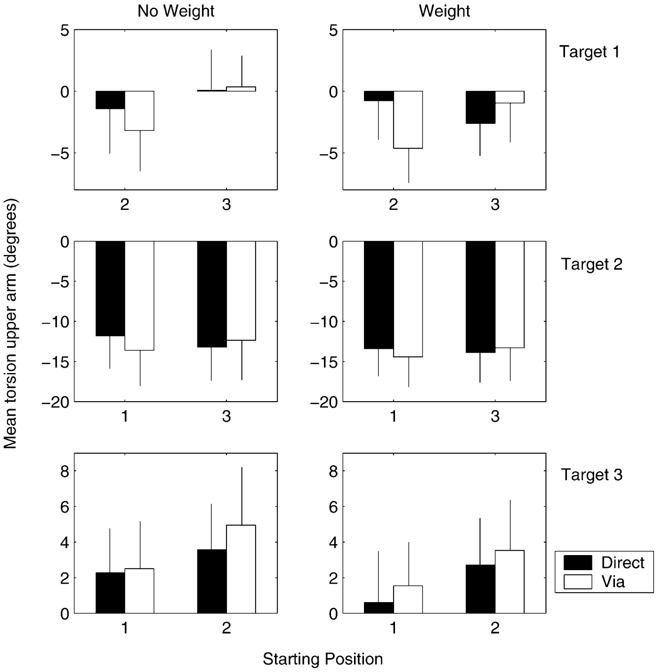


Fig. 2 Mean torsion (in degrees) of the upper arm across participants in the 'no weight' condition and the 'weight' condition. The *lines* on top of the bars show the size of the 95% confidence interval. The *solid* and the *open bars* refer to direct and 'via' movements, respectively. Numbers along the horizontal axis refer to starting position for direct and indirect movements to the target

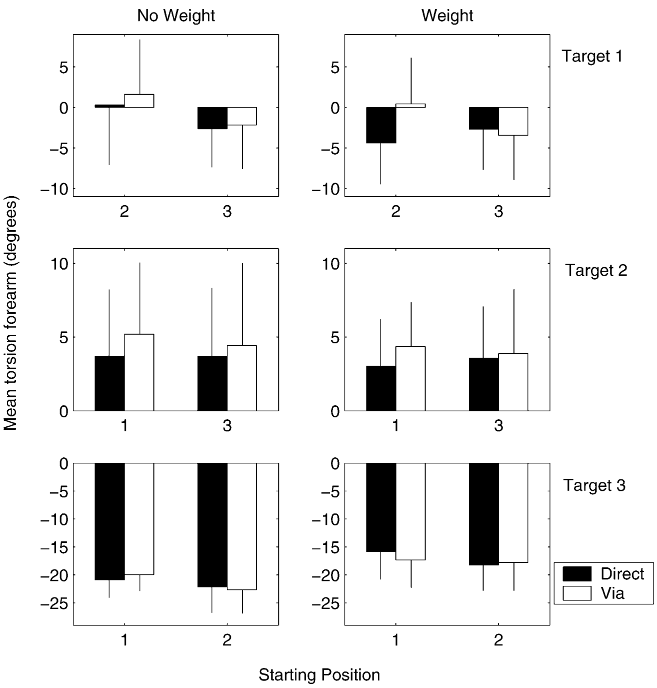


Fig. 3 Mean torsion (in degrees) of the forearm across participants in the 'no weight' condition and the 'weight' condition. The *lines* on top of the bars show the size of the 95% confidence interval. The *solid* and the *open bars* refer to direct and 'via' movements, respectively. Numbers along the horizontal axis refer to starting position for direct and indirect movements to the target

mean torsion of the upper arm ($F_{(1,9)}$=5.567, p =0.043). On forearm torsion the main effect of path was significant ($F_{(1,9)}$=5.612, p =0.042). For the upper right target a significant path-by-starting-position interaction was found on upper arm torsion ($F_{(1,9)}$=12.951, p =0.006). The only significant effect on forearm torsion was a main effect of path ($F_{(1,9)}$=7.315, p =0.024). For the upper left target both main effects of path ($F_{(1,9)}$=20.713, p =0.001) and starting position ($F_{(1,9)}$=30.437, p <0.001) were significant.

Figures 4 and 5 show the mean torsion of upper arm and forearm for the two speed conditions. In an analysis of variance the effects of movement speed, starting position, and path towards the target position were tested. Small, but significant effects of starting position and path towards the target position were found for all targets both on forearm and upper arm torsion for both movement velocities. For the two upper targets interaction effects of starting position and velocity, or of path and velocity were found.

In more detail, significant path by starting position interaction effects on upper arm torsion ($F_{(1,9)}$=6.621, p =0.030) and forearm torsion ($F_{(1,9)}$=6.831, p =0.028) were found for the bottom target. For the upper right target there was a significant path-by-starting-position interaction effect on upper arm torsion ($F_{(1,9)}$=8.146, p =0.019). On forearm torsion there was a significant path-by-velocity interaction effect ($F_{(1,9)}$=9.005, p =0.015). The two main effects of path ($F_{(1,9)}$=6.970, p =0.027) and starting position ($F_{(1,9)}$=11.126, p =0.009) on forearm torsion were significant. The upper left target showed a significant

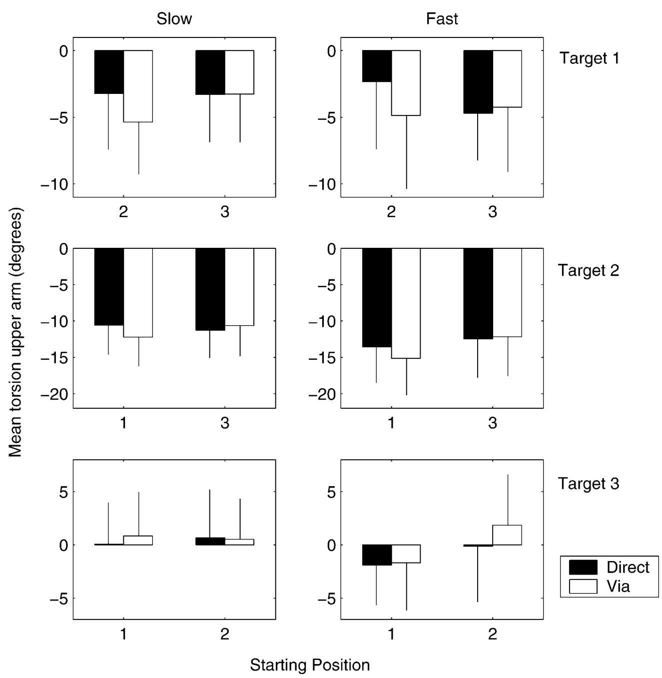


Fig. 4 Mean torsion (in degrees) of the upper arm across participants in slow speed and fast speed conditions. The *lines* on top of the bars show the size of the 95% confidence interval. The *solid* and the *open bars* refer to direct and 'via' movements, respectively. Numbers along the horizontal axis refer to starting position for direct and indirect movements to the target

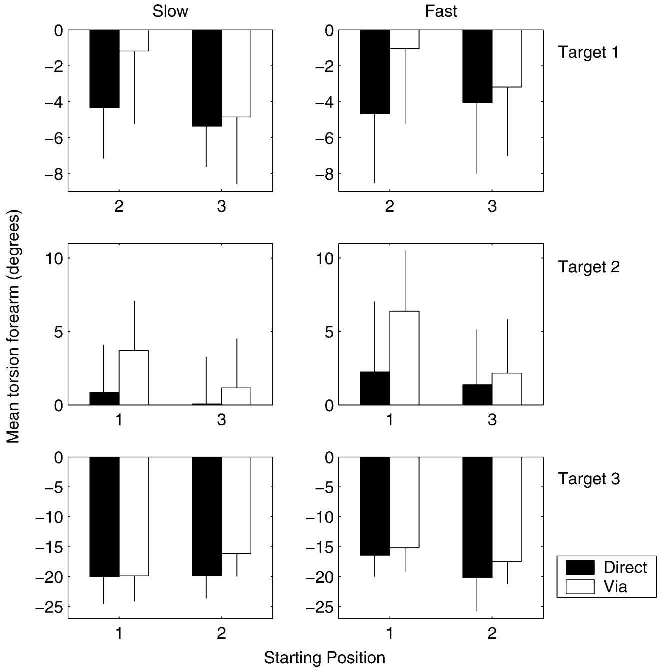


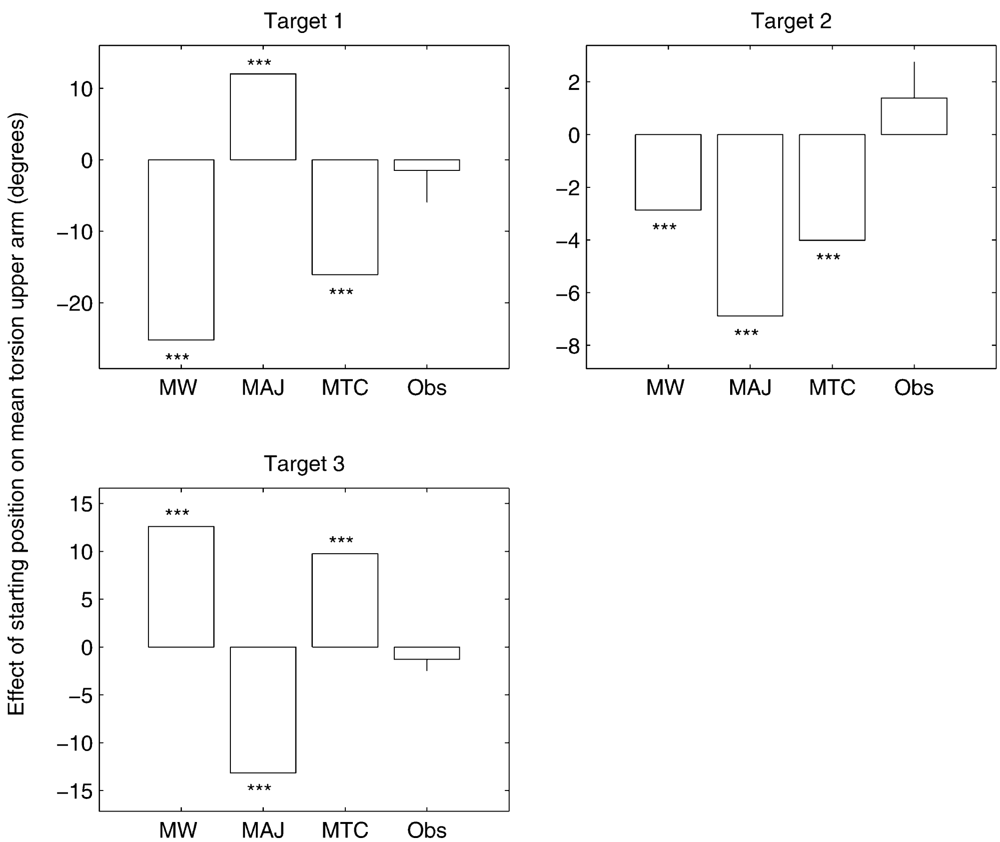
Fig. 5 Mean torsion (in degrees) of the forearm across participants in slow speed and fast speed conditions. The *lines* on top of the bars show the size of the 95% confidence interval. The *solid* and the *open bars* refer to direct and 'via' movements, respectively. Numbers along the horizontal axis refer to starting position for direct and indirect movements to the target

velocity-by-starting position interaction on upper arm torsion ($F_{(1,9)}$=5.699, p =0.041). Significant main effects of starting position (F =7.897, p =0.020) and path ($F_{(1,9)}$=5.713, p =0.041) were found. On forearm position there was a significant velocity-by-starting position interaction ($F_{(1,9)}$=12.552, p =0.006) and a significant main effect of path ($F_{(1,9)}$=8.432, p =0.017).

Model simulations

As described in the method section we compared predictions by the minimum work model, the minimum angular jerk model, and the minimum travel cost model regarding the effects of starting position, and the path taken towards the target position. These predictions were compared with the null hypothesis (Donders' law) that starting position and the path taken towards the target position do not affect final posture. Figure 6 shows predicted and observed effects of starting position for direct movements (i.e., no via-point) on arm torsion at the end of the movement. The plot shows that the minimum work model, the minimum angular jerk model, and the minimum travel cost model predict larger effects of starting position on the final posture of the arm than actually observed. The absolute errors between model predictions and observed data were considerably smaller for the minimum angular jerk model and the minimum travel cost model than for the minimum work model. Statistical tests showed that also the null hypothesis was

Fig. 6 Predicted and observed effects of starting position on the torsion of the arm at the end of the movement for direct movements from two different start positions for each target. For each target position the difference (in degrees) between the torsion at the end of the movement for the two starting positions is shown. This implies that the panel for target 1 shows the difference in upper arm orientation to target 1, starting from targets 2 and 3. *MW, MAJ,* and *MTC* refer to the predictions of the minimum work model, the minimum angular jerk model, and the minimum travel cost model, respectively. *Obs* refers to the observed effects. The *vertical lines* on top of the bars for the observed data show the 95% confidence interval. The *asterisks* near the bars of the predicted values show the results of t-tests testing whether the predicted mean was significantly different from the observed mean. A *triple asterisk* denotes a significant deviation at the p <0.001 level



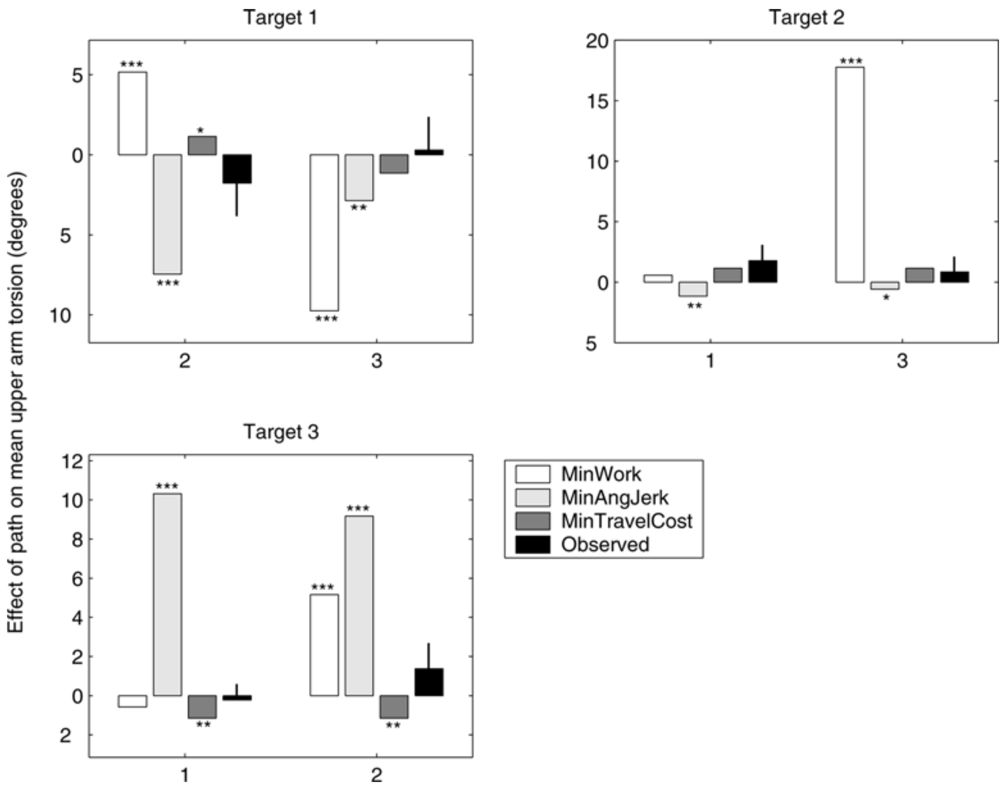


Fig. 7 Predicted and observed effects of path towards the target position on the torsion of the arm at the end of the movement. For each target position and each starting position, the difference (in degrees) between the torsion at the end of the movement for the direct and the 'via' movement is shown. *MW, MAJ,* and *MTC* refer to the prediction for the minimum work model, the minimum angular jerk model, and the minimum travel cost model, respectively. *Obs* refers to the observed effects. The small *vertical lines* on top of the bars for the observed data show the 95% confidence interval. *Numbers* along the horizontal axis refer to starting position for direct and indirect movements to the target. The *asterisks* near the bars of the predicted values show the results of t-tests testing whether the predicted mean was significantly different from the observed mean. A *single asterisk* represents a significant deviation at the $p < 0.05$ level. *Double* and *triple asterisks* denote significant deviations at the $p < 0.01$ and $p < 0.001$ level, respectively

Table 1 Summary of experimental results and model predictions. The table lists the effects of starting position, path towards the goal, movement speed and weight attached to the forearm on the posture of the arm at the end of the movement. A *question mark* indicates that no specific predictions are made by the model, or that the simulations results of the model are unknown

	Effect of starting position	Effect of path to goal	Effect of movement velocity	Effect of inertia
Experiment				
This study	Yes	Yes	No	No
Soechting et al. 1995	Yes	-	-	-
Gielen et al. 1997	Yes	-	-	-
Desmurget et al. 1998	Yes	-	-	-
Desmurget et al. 1995	-	No	-	-
Desmurget and Prablanc 1997	-	No	-	-
Grea et al. 2000	-	No	-	-
Nishikawa et al. 1999	-	-	No	-
Flanders et al. 2003	-	-	-	Yes
Fischer et al. 1997	-	-	No	-
Model				
Donders' law	No	No	No	No
EP Hypothesis	?	?	No	No
Minimum angular jerk	Yes	Yes	Yes	No
Minimum torque-change	Yes	Yes	?	Yes
Minimum work	Yes	Yes	No	Yes
Minimum variance	Yes	Yes	?	?
Knowledge model	Yes	Yes	Yes	No

violated. In terms of absolute errors the null hypothesis (Donders' law) still gave the best description of the data.

Figure 7 shows the predictions of the models and the observed effects of movements along a via-point towards the target position on the torsion of the arm at the end of the movement. The minimum work model shows large overestimations of the effect of the path towards the target. The minimum angular jerk model and the minimum travel cost model gave a better fit of the observed data.

Discussion

Table 1 presents an overview of the experimental results obtained in this study, and of results obtained by previous studies. Moreover, it shows the predictions by various models. In the table we included qualitative predictions of Donders' law (Von Helmholtz 1867), the equilibrium point (EP) hypothesis (Feldman and Levin 1995), the minimum angular jerk model (Wada et al. 2001), the minimum torque-change model (Uno et al. 1989), the minimum work model (Soechting et al. 1995), the minimum variance model (Harris and Wolpert 1998), and the knowledge model (Rosenbaum et al. 1995).

For the EP hypothesis it is hard to make reliable predictions for all conditions. At the muscle level and the joint level the predictions by the EP hypothesis have been clearly spelled out. However, this is not the case for multi-joint movements. The only report regarding the extension of the EP hypothesis to multi-joint movements is the study by Lestienne et al. (2000). However, this study does not allow the extension of this hypothesis to complex movements such as the four degrees of freedom arm movements in our study. Two predictions for the EP hypothesis can be made for our data set: the final arm posture will depend neither on the movement velocity, nor the loading of the arm (see also Jaric et al. 1999).

It is well known that rotations in 3-D do not commute (see e.g., Tweed and Villis 1987). Therefore, the orientation of the arm after two single-axis rotations depends on the order of the rotations. As a consequence, the orientation of the fully extended arm after a single-axis rotation in the shoulder along the shortest path starting from a particular posture to a target will differ from the orientation of the arm after two single-axis rotations along the shortest path from the same initial posture to the same target by a via-point (see Stoker 1969). As a consequence, all models that predict single-axis rotations along a shortest path for the fully extended arm (such as the minimum angular jerk model, the minimum work model, the minimum torque-change model, and the minimum variance model) will predict an effect of starting position, and of the path towards the goal (direct movement or through a via-point). For similar reasons these models also predict an effect of starting position and path towards the goal for arm movements with elbow flexion.

The equations for minimum angular jerk and minimum travel cost (part of the knowledge model) depend on the movement time. It can be shown that the minimum work model does not predict an effect of movement time (Nishikawa et al. 1999). The angular jerk model and the knowledge model predict small effects of movement velocity on the final posture of the arm.

Because the inertia of the arm plays an important role both for the minimum work model and the minimum torque-change model, these models predict that the final posture of the arm depends on the weight of the forearm. The equations of minimum angular jerk, and minimum travel cost do not depend on the weight attached to the arm segments, and therefore predict no effect of the weight of the forearm.

Our study replicated the effects of starting position on the final arm posture reported in previous studies (Desmurget et al. 1998; Gielen et al. 1997; Soechting et al. 1995). All studies that have tested the effect of starting position have reported an effect of starting position. These observations argue against Donders' law, which predicts a unique posture of the arm for each position of the finger in 3-D space, independent of previous postures. Simulations with the minimum work model, the minimum angular jerk model, and the minimum travel cost model show that these three models predict larger effects of starting position than actually observed. The observation that the minimum work model predicts larger effect of starting position than observed corresponds to earlier reports by Vetter et al. (2002) and by Klein Breteler et al. (2003). For our data set, the minimum work model not only predicts too large effects, but also the direction of the effects is not correctly predicted.

In the present study, small but significant effects were found of the path taken towards the target position on the posture of the arm at the end of the movement. These effects relate to previous findings by Desmurget and colleagues (Desmurget and Prablanc 1997; Desmurget et al. 1995; Grea et al. 2000), where a change in target position or orientation after movement onset resulted in a different path to the target for perturbed and unperturbed trials. In their study no effect of a target change was found on the posture of the arm at the end of the movement. This result may seem contradictory to the results in our study. However, this discrepancy can be resolved if we consider the size of the effect. In the studies by Desmurget and colleagues the change in target position led to relatively small differences in movement trajectory. The differences in path were much smaller than the differences in path for the direct movements and for movements along a via-point in our study, where the effects of path were small. Therefore, we speculate that any effects of path in the study by Desmurget were too small to be observed in their study.

No effects of movement velocity were found, which is in agreement by earlier findings by Nishikawa et al. (1999), but at odds with findings by Fischer et al. (1997). However, Fischer et al. (1997) used rhythmic repeated movements, which have properties that differ from those of discrete movements (Schaal et al. 2001).

We did not find an effect of the weight attached to the forearm on the posture of the arm at the end of the movement in this study. In a previous study Flanders et al. (2003) reported an effect of a rod with a weight of 0.46 kg attached to the upper arm on the initial posture. A possible explanation for the different results might be that subjects are used to making movements with objects of different weights at their hand, which basically corresponds to the situation with the weight at the wrist in our study. Flanders et al. (2003) attached a weight to the upper arm some distance away from the long axis through the upper arm. In their study the weight was attached to the upper arm because simulations suggested that more conventional weights (such as the weight symmetrically distributed around the wrist) would not significantly alter the mass distribution and therefore the predictions of the minimum work model. To investigate whether the absence of a significant effect of the weight attached to the forearm found in our study provides evidence against the minimum work model, we did some additional simulations with the model. These simulations showed that the predicted effect of the weight attached to the wrist was on the order of a few degrees. Since the effect found in our study was on the same order, it may have been too small to reach significance.

Previous research by Shadmehr and Mussa-Ivaldi (1994) investigated the adaptation to more complex changes of the arm dynamics. In their study participants adapted to a force applied to the hand during reaching movements. In the first few trials the force applied to the hand strongly affected the hand trajectories. After some practice hand paths became smoother and resembled those of reaching movements without a force applied to the hand. If participants moved according to a minimum work or a minimum torque-change strategy, such an adaptation would not take place.

To conclude, none of the models considered could fully account for the data observed. Our study indicates that future tests of models for motor control should compare the predictions of several models for a single, large data set, and that the comparison should include movements in 3-D, rather than in 2-D.

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