

Posture-based or trajectory-based movement planning? A comparison of direct and indirect pointing movements

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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 demonstrate that for future tests of models of motor control (1) it is important to compare the predictions of not only one, but several models to a data set, (2) not only planar, but also 3D movements should be considered in such a comparison.¹

Keywords: Motor control, Arm movements, Pointing, Movement planning

Introduction

Various models have been proposed to explain the planning and execution of arm movements (Feldman & Levin, 1995; Gielen, Vrijenhoek, Flash, & Neggers, 1997; Harris & Wolpert, 1998; Soechting, Buneo, Herrmann, & Flanders, 1995; Rosenbaum, Loukopoulos, Meulenbroek, Vaughan, & Engelbrecht, 1995; Rosenbaum, Meulenbroek, Jansen, & Vaughan, 2001; Uno, Kawato, & Suzuki, 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 initial posture and final 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 & Levin, 1995) (Note that Donders' law is more strict in that the final posture is not predicted to be dependent on the initial posture³).

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 & Wolpert, 1998). The knowledge model to postulate a new model to account for the cure 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

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³ Sentence added to clarify point by Reviewer 2

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 presented evidence 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, Flash, and Wolpert (2002) who asked participants to touch a target bar using a hand-held 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, Desmurget, & Prablanc, 2000) tried to discriminate between the two classes of models by investigating the effect of a change in target position or target orientation after movement onset on the final arm posture. In the study by Desmurget, Prablanc, Rossetti, Arzi, Paulignan, Urquizar, and Mignot (1995) participants were asked to grasp a bar of which the orientation changed at movement onset in a proportion of the trials. A similar task was used by Desmurget, Grea, and Prablanc (1998) who asked participants to grasp a bar from different starting positions. Also in this study the orientation of the bar could at movement onset. Grea, Desmurget, Prablanc (2000) asked participants grasp a sphere. In some trials the position of the sphere changed at movement onset. By changing the target position or the target orientation at movement onset, the observed movement trajectories changed with respect to those in unperturbed movements.⁴ Trajectory-based models would predict the final posture of the arm to depend on whether the target object would rotate or change its position at movement onset. No such dependence of the final arm posture on the change of position or orientation was found.⁵ (Desmurget et al., 1995; Desmurget & Prablanc, 1997). No effect was found of the initial position of the sphere to be grasped on the final posture of the arm when the position of a sphere was changed after movement onset (Grea et al., 2000). These results argue in favor of posture-based models, like Donders' law. Note that the study by Desmurget et al. (1998) provided both evidence in favor of and against Donders' law. The lack of an effect of an orientation or position change on the final arm posture argues in favor of Donders' law. However, the effect of the initial posture of the arm on the final arm posture presents evidence against Donders' law.⁶

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 (Soechting et al., 1995; Gielen et al., 1997; Desmurget et al., 1998; 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, Kaneko, Nakano, Osu, & Kawato, 2001). Following our definition of posture-based and trajectory-based models, the best way to discriminate between posture-based and trajectory-based planning is investigated the effect of the path towards the goal position on the final arm posture. Trajectory-based models predict the final arm posture to depend on the path taken, while posture-based models predict the final arm posture to be independent of the path. To our knowledge, this test and a quantitative comparison with predictions by various models 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 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. If participants move according to a trajectory-based model the final posture for a target position is expected to depend on the path taken.

To allow for a detailed comparison between 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, Murray, and Flanders (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,

⁴ Description of experiments added. Request of the 1st reviewer, page 2. Following sentence altered to fit the next sentences in.

⁵ I changed this sentence completely. Both Reviewer 2 and David Rosenbaum found the sentence confusing.

⁶ Added. Request by Reviewer 1.

whereas posture-based models, such as Donders' law, do not predict an effect.

In our study we chose to make a comparison of several models based on their predictions for one data set. By doing so, we ignored each of the models' background, and the kind of data they are aiming to describe. For example, the EP hypothesis was developed to account for muscle properties, reflexes, and their effects on final postures. Donders' law originated from the study of eye movement control (Haslwanter, 1995). The knowledge model was developed to account for psychological aspects of motor control, such as memory effects. We think that a objective comparison of the performance of several models of motor control is useful, irrespective of the history and previous demonstrations of the models to account for certain data sets. In general arm movements are expected to be planned to be smooth, not to produce large joint torques, and to require little energy. By comparing the various models with one data set we can determine which criterium, if any, is used to plan movements⁷.

Method

Experiment

Participants.

In each experimental condition 10 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 tasks⁸. The age of the participants ranged from 16 to 56 (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 of the 16 years old was approved by his parents⁹.

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 by 2 meter vertical projection screen. Stimuli were presented within a 115 by 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 5 IREDS each with a distance of 4

cm between the two rings. The remaining 4 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. Using the programs Rigmaker and Rigid provided with the Optotrak system the orientation and location of each bracelet was determined. The orientation of each bracelet could be measured with an accuracy better than 0.5 degrees.

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 Figure 1. Each of the stimuli could either serve as a target or a via point. All stimuli were presented within a distance of 70 cm from the shoulder. Panel A of Figure 1 shows a top view of the participant and the screen. Participants were facing the projection screen under an angle to allow for reaching the upper left stimulus. If the projection screen would not have been under an angle, the participant's body would be in the way. Panel B 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 frame centered at the right shoulder, with the horizontal axis connecting the two shoulders. The center target (target 4) was at coordinates (51, -15, 17), the upper left target (target 3) was at (63, 38, 30), the upper right target (target 2) coordinates were (39, -36, 29), and the bottom target (target 1) was at (52, -19, -11). All distances with respect to the shoulder were measured in cm¹⁰.

The orientation of upper arm and forearm at each target was expressed as a rotation vector (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

⁷ Text added. Mark Latash and David Rosenbaum did not like the fact that we compared the models using this one data set. Also Reviewer 1 commented that there is no solid background for Donders' law. I would have this comment for all the optimization models too... The statement I put down here now, might need to be rephrased. I will think about it later again.

⁸ Again, changed, David Rosenbaum was confused by the sentence

⁹ Sentence added. Necessary in US experiments.

¹⁰ The figure and the description of the stimuli was changed. Reviewer 2 and David Rosenbaum suggested this would be better. I replaced the word 'targets' with 'stimuli' to clarify the fact that each point could both serve as a target and a via point.

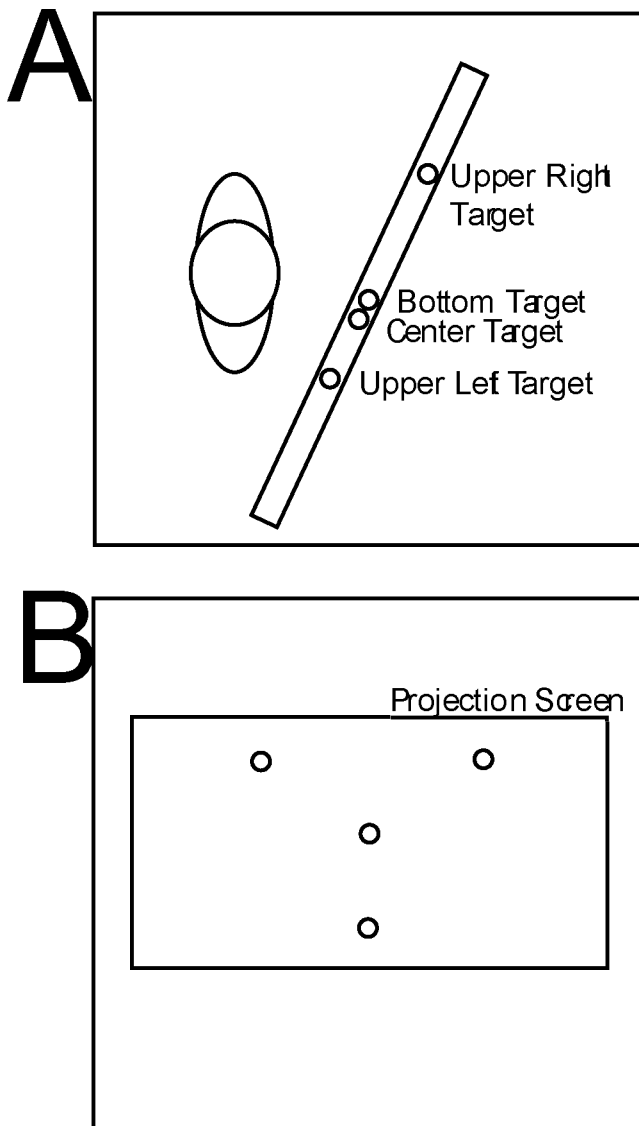


Figure 1. The position of the stimuli in the experiment. The stimuli were projected on projection screen which participants viewed under and angle (Panel A). The projected stimuli were organized in a triangle with respect to each other, with the reference stimulus in the center (Panel B).

speed¹¹) (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 seconds. In the 'no weight' and 'weight' conditions the inter-trial time was 2 seconds, while in the 'slow' condition an inter-trial time of 2.5 seconds 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 the 'fast' condition 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 8 blocks with 25 trials each were presented. At the first trial of each block the central target (number 4) 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.

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:

¹¹ Added part on movement instruction, recommended by David Rosenbaum

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

Here ϕ represents the elbow flexion angle ($\phi = 0$ 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 $\Omega_x, \Omega_y, \Omega_z$, see Soechting et al. (1995). Like Soechting et al. (1995) 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:

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

where the θ_i represent the joint angles (flexion/extension of the elbow, and three orthogonal rotation axes at the shoulder), and t_f denotes the duration of the movement. The path in joint space according to this criterion is a fifth order spline.

The minimum travel cost criterion is copied from Rosenbaum et al. (1995, 2001). If an infinite planning time is assumed for the 2001 version of the model, exhaustive search gives the minimum travel cost. This 'infinite planning time' is only a theoretical option. The infinite planning time shows what the model would predict in the limit¹². The travel cost is computed by the following equation:

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

where α_j is the angular joint rotation¹³. k_j are constants related to the joint stiffness. We set these constants equal to 1 (see 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 degrees to 180 degrees in steps of 1 degree, 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 the 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 function¹⁴.

For the comparison of the data for the 'no weight' condition with the model predictions we used a movement duration of 1 second. 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 (target 4). Bars indicate the mean torsion across subjects. Lines on top of the bars represent the 95% confidence intervals across participants.

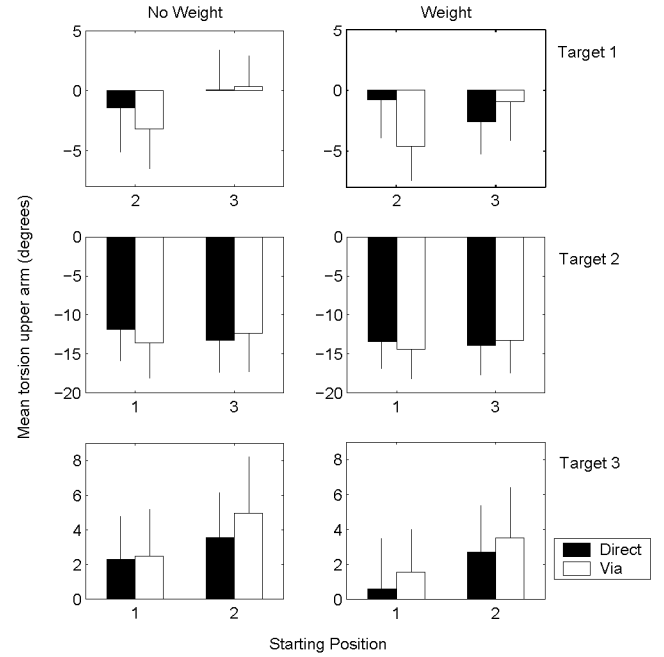


Figure 2. Mean torsion (in degrees) of the upper arm across participants in the 'no weight' condition and the 'weight' condition. The lines on top of the bars show the size of the 95% confidence interval. The solid and the open bars refer to direct and 'via' movements respectively. Numbers along the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

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. Note that these ANOVAs in fact test whether Donders' law can accurately describe the data. By predicting no effects of starting position, path towards the goal position, and the weight attached to the forearm, Donders' law predicts equal final end postures for each of the experimental conditions¹⁵.

¹² Sentence added. Comment by Reviewer 1

¹³ Word added. Indeed there are 4 possible joint rotations, not joints.

¹⁴ 'Criterium' replaced by 'cost function'. Additionally the compared models were specified (Reviewer 1)

¹⁵ Added to clarify the statement made by Reviewer 1, about the "Null hypothesis", page 1. Tests of the other models need to be

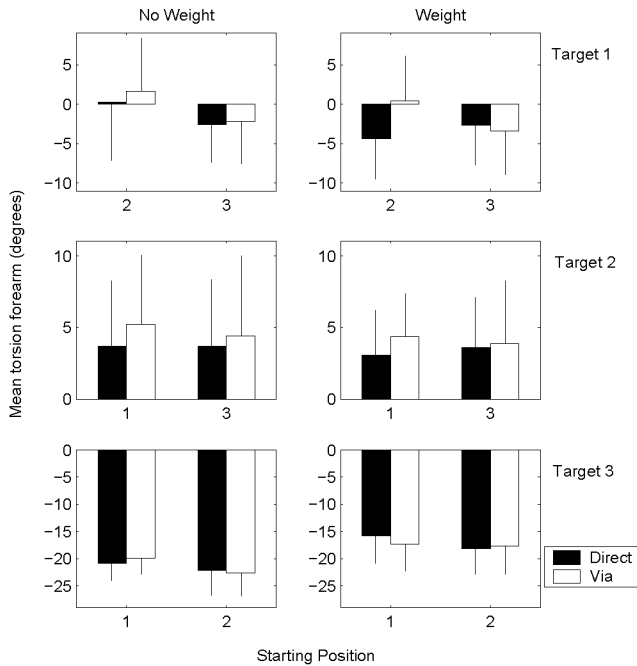


Figure 3. Mean torsion (in degrees) of the forearm across participants in the 'no weight' condition and the 'weight' condition. The lines on top of the bars show the size of the 95% confidence interval. The solid and the open bars refer to direct and 'via' movements, respectively. Numbers along the horizontal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

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 (target 1) a significant interaction effect was found of path and starting position on the 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 (targets 2 and 3) interaction effects of starting position and velocity, or of path and velocity were found.

In more detail, significant path by starting position inter-

action 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 (target 1). For the upper right target (target 2) 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 (target 3) showed a significant 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 ($F(1,9) = 8.432$, $p = 0.017$).

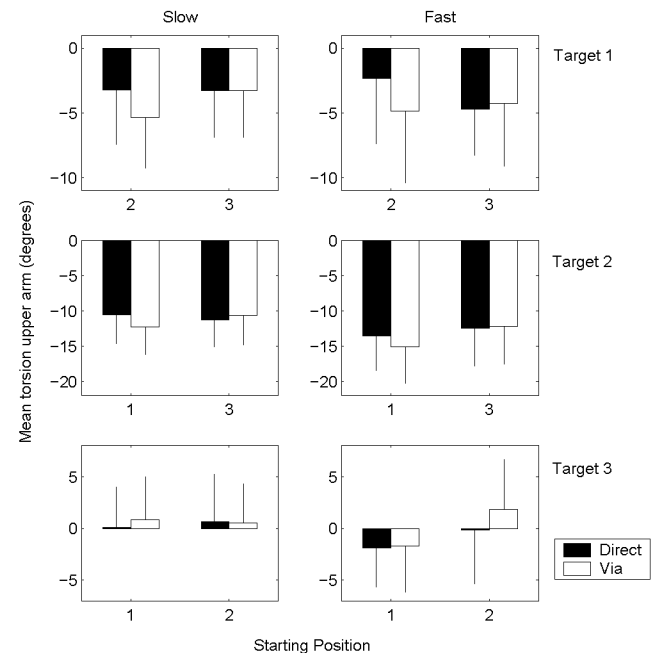


Figure 4. Mean torsion of the upper arm across participants in slow speed and fast speed conditions. The lines on top of the bars show the size of the 95% confidence interval. The solid and the open bars refer to direct and 'via' movements respectively. Numbers along the horizontal axis refer to starting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

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

added. For that, I will need the subject means per condition. I am planning to add the results of these test to the models section.

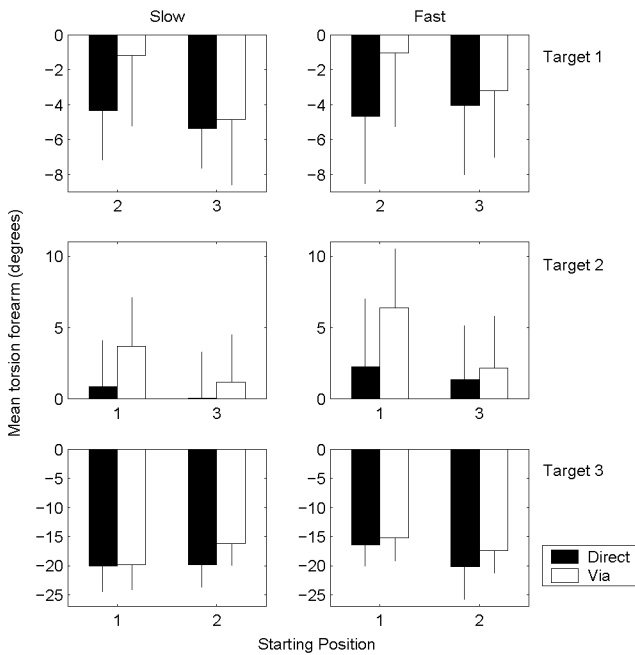


Figure 5. Mean torsion of the forearm across participants in slow speed and fast speed conditions. The lines on top of the bars show the size of the 95% confidence interval. The solid and the open bars refer to direct and 'via' movements respectively. Numbers along the horizontal axis refer to starting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

the effects of starting position, and the path taken towards the target position. The fourth model, Donders' law, predicts no effects of starting position and the path taken towards the target position. 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. However, by predicting no effect of starting position and of the path towards the target, Donders' law fits the data quantitatively better than any of the other three models.

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.

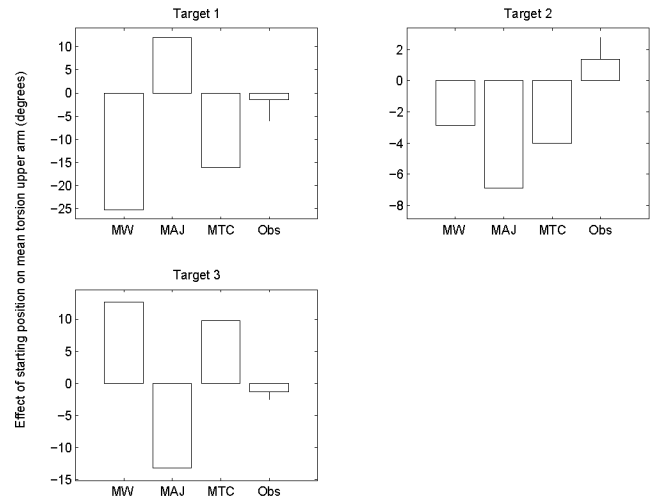


Figure 6. Predicted and observed effects of starting position on the torsion of the arm at the end of the movement for direct movements from two different start positions for each target. For each target position the difference (in degrees) between the torsion at the end of the movement for the two starting 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.

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 hypothesis (Feldman & 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 & Wolpert, 1998), and the knowledge model (Rosenbaum et al., 1995).

Of the models we classified as posture-based, Donders' law predicts no effects of movement velocity, the path towards the goal position, the starting position, or the weight attached to the forearm. What the predictions of the EP hypothesis are, is less clear. At the muscle level and the joint level the predictions by the EP hypothesis have been clearly spelled out. This is not the case for multi-joint movements. Lestienne, Thullier, Archambault, Levin, and Feldman (?) proposed a referent configuration hypothesis, but it is not clear how to extend this hypothesis to complex movements, such as the four degrees of freedom movements observed in our study. Two predictions for the EP hypothesis can be made for our data set: The final arm posture will not depend on the movement velocity, and on the loading of the

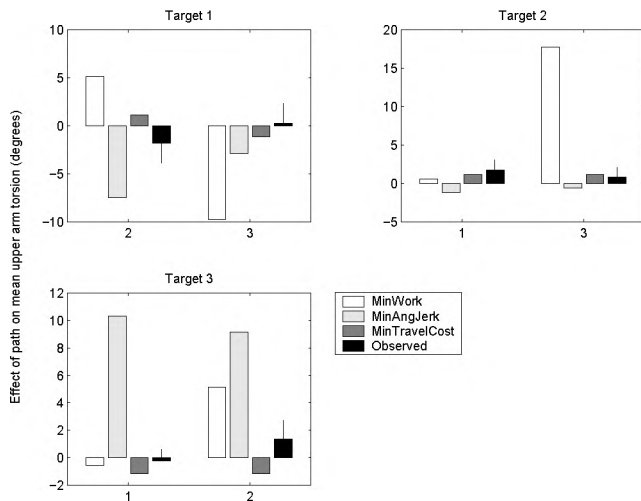


Figure 7. Predicted and observed effects of path towards the target position on the torsion of the arm at the end of the movement. For each target position and each starting position the difference (in degrees) between the torsion at the end of the movement for the direct and the 'via' movement is shown. 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.

arm (?see also)jaric99¹⁶.

It is well known that rotations in 3-D do not commute (see e.g., Tweed & Vilis, 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, which 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 found in previous studies (Desmurget et al., 1998; Gielen et al., 1997; Soechting et al., 1995). All studies, which 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, Flash, and Wolpert (2002), and by Klein Breteler et al. (2003).¹⁷ Altogether, the results indicate that none of the models considered here can provide a quantitatively correct prediction of the effect of start position. None of the models was able to predict the pattern of results¹⁸. The model, which gives the best predictions, based on an absolute error between predicted and measured arm postures, is Donders' law.

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 et al., 1995; Desmurget & Prablanc, 1997; Grea et al., 2000), where a change in the orientation of the 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 et al. 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, Rosenbaum, and Vaughan (1997). The fact that Fischer et al. (1997) found effects might be due to the rhythmic repeated movements that they used in their study, in contrast to the discrete movements used in our

¹⁶Section added. Reviewer 1 asks for more text on the EP hypothesis. References provided by Mark Latash included.

¹⁷Reference added, reviewer 2.

¹⁸Added to stress that the size differences are not the only ones

Table 1

	Effect of start- ing position	Effect of path to goal	Effect of movement velocity	Effect of iner- tia
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 et al., 1997		No		
Grea et al., 2000		No		
Nishikawa et al., 1999			No	
Flanders et al., 2003				Yes
Fischer et al., 1997			Yes	
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

study and the study by Nishikawa et al. (1999)¹⁹.

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, Hondzinski, Soechting, and Jackson (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. Subjects might not be used to such loads. Simulations with the minimum work model show that this model predicts small effects of the weight attached to the wrist, on the order of a few degrees. The effects in our study were on the same order, although they did not reach significance. The effects found by Flanders et al. (2003) of a few degrees in size are compatible with the predictions by the minimum work model. In our experiment participants quickly adapted to the weight attached to the wrist, typically within a few trials. Previous research by Shadmehr and Mussa-Ivaldi (1994) investigated the adaptation to more complex changes of the arm dynamics. The adaptation of the movement trajectory to the unperturbed trajectory suggests that a minimum work principle or minimum torque-change principle cannot account for all reaching movements data. 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 could fully account for the data observed. To postulate a new model to account for the observed data would make little sense: This would be mere data fitting. Our study, however, shows that in future tests of models of motor control (1) one should compare predictions of several models with a single data set, (2) it is important to include 3D movements in the comparison²⁰.

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¹⁹ Reference added, suggested by David Rosenbaum. That there is a difference between rhythmic and discrete arm movements, was demonstrated by Sternad and colleagues, but seems not to have been published yet

²⁰ Conclusion modified. Reviewer 1 correctly points out proposing a combination of posture-based and trajectory-based models would probably make little sense (page 1, bottom). David Rosenbaum, in a first response, proposed to describe a model to explain for the current data set. Also, I added something Reviewer 2 pointed out: The addition of 3D movement data to our data set.

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Table Captions

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.