Abstract

It is currently unclear whether the brain plans movement kinematics explicitly, or whether movement paths arise implicitly through optimization of a cost function that takes into account control and/or dynamic variables. Several cost functions are proposed in the literature that are very different in nature (e.g. Control Effort, Torque Change and Jerk), yet each can predict common movement characteristics. Here we set out to disentangle predictions of the different
variables using a combination of modeling and empirical studies. Subjects performed goal
directed arm movements in a force field (FF) in combination with visual perturbations of seen
hand position. This FF was designed to have distinct optimal movements for muscle-input and
dynamic costs, while leaving kinematic cost unchanged. Visual perturbations in turn changed the
kinematic cost, but left the dynamical and muscle-input costs unchanged. An optimally
controlled physiologically realistic arm model was used to predict movements under the various
cost variables. Experimental results were not consistent with a cost function containing any of
the control and dynamic costs investigated. Movement patterns of all experimental conditions
were adequately predicted by a kinematic cost function comprised of both visually and
somatosensory perceived jerk. The present study provides clear behavioral evidence that the
brain solves kinematic and mechanical redundancy in separate steps: in a first step movement
kinematics are planned and in a second separate step muscle activation patterns are generated.

Keywords: motor control, motor learning, force field, control effort, jerk, torque change, muscle
energy, muscle activation patterns, arm kinematics.

Introduction

It is suggested in the literature that the brain computes muscle activation patterns that minimize a
task relevant cost function (e.g. Flash and Hogan 1985; Hasan 1986; Todorov 2004). The most
important cost variables put forward in the literature can be categorized in three distinct levels: a
control (muscle-input) level, a dynamic level and a kinematic level. At the control level there is,
for example, control effort –i.e. the sum of squared muscle activation– (Fagg et al. 2002;
Todorov 2002; van Bolhuis and Gielen 1999) and has been theorized to minimize end-point
variance due to signal dependent noise (Diedrichsen et al. 2010; Harris and Wolpert 1998). Two
influential variables at the dynamic level are torque change (Uno et al. 1989) and energy
expenditure (Alexander 1997; Kistemaker et al. 2010). At the kinematic level there is one
important variable: jerk –the time derivative of acceleration–, proposed to capture common
invariant kinematic features observed experimentally (Flash and Hogan 1985). All of these cost
variables have been successful at predicting common kinematics of human movements in free
space (here taken as movements performed in an inertial reference frame without additional
forces applied to the moving limb), even though they are very different in nature. As a result it is experimentally impractical to discern if and what unique cost function may be used by the brain.

Evidence exists in the literature that (visual) kinematics play an important role in movement planning. For example, Thoroughman et al. (2007) showed human arm movements performed in a robot-induced force-field after learning were consistent with minimization of kinematic jerk, but not with minimizing either endpoint variance or minimal torque change. In addition, Wolpert and colleagues (1995) used a simple yet very clever experimental setup to artificially increase the curvature of the seen hand trajectory. Even though subjects did not need to change their muscle activation patterns to reach the targets, it was found that participants moved to reduce the visual perturbation. These results clearly suggest that kinematic variables play an important role in kinematic planning. However, it does not exclude the possibility that dynamic and/or control variables may also play a role. Furthermore, Todorov and Jordan (2002) theorized that due to the systematic discrepancy introduced between "expected and received feedback", the internal model that generates motor commands undergoes changes, which may lead to adaptation in kinematic planning.

The goal of the present study was to investigate the role that control, dynamic and kinematic variables play in movement planning. To do so, we designed a combined virtual and mechanical environment that allowed us to independently manipulate cost variables at a control, dynamic and kinematic level. Subjects moved in a force-field (FF) induced by a robotic manipulandum at different strengths while being visually perturbed. We used Optimal Control (see Optimization) to find optimal muscle activations for a detailed musculoskeletal model of the arm that included, amongst others, non-linear activation dynamics accounting for the electromechanical delay and muscle activation level dependent optimum lengths, non-linear elastic tendon forces and non-linear force-length-velocity relationships of muscle fibers (Kistemaker et al. 2006; Kistemaker et al. 2010). This model was used to predict arm kinematics that minimized various cost variables at the level of muscle activation (e.g., sum of squared muscle activation and min/max), at the level of dynamics (e.g. muscle torque change, muscle fatigue) and at the level of kinematics (jerk).

The experimental and model results of this study strongly suggest that neither control variables nor dynamical variables play an important role in kinematic planning of human arm
movements. The paths taken by the subjects are only consistent with a cost function that is comprised solely of kinematic variables.

Methods

Ethics Statement

All subjects reported no history of visual, neurological or musculoskeletal disorder. Written informed consent was obtained from each subject prior to participation. All procedures were approved by the University of Western Ontario Research Ethics Board.

Experimental setup

Subjects made movements while grasping the handle of an InMotion robotic manipulandum (Interactive Motion Technologies, Cambridge, MA, see Figure 1A). Commanded forces to the robot were adjusted to compensate for position dependency of the robot arm’s inertia to create an isotropic inertial characteristic with a mass of 1 kg. This was done using an inverse model of the inertial properties of the robot to calculate the force applied to the hand, such that the total handle force that a subject experiences equals that of accelerating an object with a mass of 1kg. The right arm was supported by a custom-made air sled, which expelled compressed air beneath the sled to minimize surface friction. The subject’s arm and the manipulandum were beneath a semi-silvered mirror, which reflected images projected by a computer controlled LCD screen. Visual targets (diameter of 2 cm) were projected which appeared to lie in the same plane as the hand. Positional and force data were sampled at 600Hz. All movements were made in the dark and only reflected images of the LCD were visible to the subjects.

Force field

The force field (FF) used in this study was similar to that used in Kistemaker et al. (2010). We had designed a new force field for several reasons. Most importantly, we wanted to make the FF such that there is a mechanical advantage (less muscle force\torque) to make movements curved markedly to the right, instead of the typical slightly leftward path taken in free space. Here we use this FF to test variables that might be used by the brain to select a kinematic path in a novel mechanical environment. The force applied at the hand in the y-direction (fore-aft; Fy) was:
\[ F_y = b(-\dot{y} + \dot{x}) \cdot |y_{\text{target}} - y| \]  
(1)

In contrast with our previous study in which we used a value of either 0 or 150 Ns/m², we have set \( b \) either to 0, 150 or 225 Ns/m². \( y_{\text{target}}, \dot{y}, \text{ and } \dot{x} \) are respectively the y-position of the target, y-position of the hand, the y velocity of the hand and the leftward/rightward (x) velocity of the hand. Note that the force in the x-direction (\( F_x \)) was always zero. For a detailed description of the FF, please see Kistemaker et al. (2010).

**Visual perturbation**

Visual warp was similar to that used in Wolpert et al. (1995) and only warped the depicted hand position along the x-axis. The depicted x-direction of the hand was the actual x-position plus a function of the y-position that defined an arc from the start position to the target position with a maximal lateral distance halfway along the y-position between the start and target. The maximal lateral distance, \( w \), was set to either 0 (no warp), 20 or 30 mm to the right or -30 mm to the left (see Fig. 1B). Note that this warp results in no visual distortion of the hand position at both the start and target position. Therefore, no correction in movement path is required to adequately reach the target. To further explain the warp, we have plotted a sample trajectory of the hand in solid lines and the accompanying visually warped hand position in dashed lines for the case that the warp was set to -30mm (Fig. 1B). This means that to make the hand go visually straight, subjects need to make a counter arc of 30 mm to the right.

To implement the visual perturbation, we calculated the perturbed visual hand position in x-direction \( (c_x) \) as a function of the actual hand position in the x-direction \( (x_h) \) and the (unperturbed) hand position in the y-direction \( (c_y=y_h) \). First, radius \( R \) of the circle was calculated leading to an apex halfway along the movement with the desired width \( w \) and movement distance \( D \):

\[ R = \frac{(0.5 \cdot D)^2 - w^2}{2w} + w \]

\( c_x \) was calculated as follows:

\[ c_x = -R \cdot \cos(\arcsin \left( \frac{y_h}{R} \right)) + R - w + x \]  
(2)
In a pilot study we investigated the maximal level of warp (gradually introduced) that was not detected by any of the participants. Several subjects reported that “something was wrong” for visual perturbations of 50 mm and greater and data analysis showed that participants ignored visual feedback altogether. Only for distortions as small as 30 mm, did none of the subjects become aware of the visual manipulation. Furthermore, after the experiments, subjects were asked if they had noticed the visual perturbation. All subjects responded in the negative and were surprised that the depicted and real hand positions did not coincide. None of the subjects in this pilot study participated in the experiment.

Experimental protocol

To ensure that the force field and associated motor costs were salient, we used FF strength levels and desired movement times that resulted in considerable forces applied to the hand. To have a uniform group of participants that experienced similar relative forces applied to their hand we restricted our selection criterion to right-handed males. Forty nine participants performed point-to-point movements to visual targets while grasping the handle of the robotic linkage with their right hand. Movements (30 cm) were made toward and away from the body in a horizontal plane along the surface of a desk, at shoulder height (see Fig. 1A). The subjects’ view of their arm was occluded by the semi-silvered mirror. Visual targets and a small dot representing the position of the hand were displayed on the mirror using an LCD monitor. When the target circle was reached, the target changed color to provide feedback indicating that the movement was either well-timed (between 300-500ms), too slow or too fast. To avoid biasing subjects to move along a particular hand path, apart from the timing aspect, no instructions were given as to how the target was to be reached. After two seconds, start and target position were swapped, and subjects initiated a new movement towards the original start position. In contrast with our previous study (Kistemaker et al. 2010), we provided continuous feedback of their hand position by plotting a small white circle (diameter 1 cm) that matched the position of the robot handle (or was warped, see above).

The subjects were randomly assigned to 7 different experimental groups, based on the strength of the force field (0, 150 or 225 Ns/m²) and level of warp (-30, 0, 20 or 30mm). The different experimental groups are shown in Table 1.
Table 1 Overview experimental groups

<table>
<thead>
<tr>
<th>group</th>
<th>FF0w2</th>
<th>FF1w0</th>
<th>FF1w2</th>
<th>FF0w3</th>
<th>FF2w0</th>
<th>FF2w3</th>
<th>FF2w-3</th>
</tr>
</thead>
<tbody>
<tr>
<td>b (Ns/m²)</td>
<td>0</td>
<td>150</td>
<td>150</td>
<td>0</td>
<td>225</td>
<td>225</td>
<td>225</td>
</tr>
<tr>
<td>W (mm)</td>
<td>20</td>
<td>0</td>
<td>20</td>
<td>30</td>
<td>0</td>
<td>30</td>
<td>-30</td>
</tr>
</tbody>
</table>

All experimental groups started first with a block in which subjects made 100 movements in free space (i.e. force field turned off; FF0) and no visual warp (w0). After that, in block 2 either 100 or 150 movements were made while gradually introducing the perturbations (both visual warp and FF) according to their experimental group. These differences in number of movements in the second block were such that the subjects had an equal gradual increase in visual warp and forces applied to the hand across the different experimental groups. Subjects that either had a FF strength of $b=150\text{Ns/m}^2$ and/or had a visual warp level of $-20$ mm had 100 movements in block 2. Subjects that either had a FF strength of $b=225\text{Ns/m}^2$ and/or had a visual warp level of $\pm30$ mm had 150 movements in block 2. In block 3 and 4, subjects always made 100 movements in the condition according to their experimental group. In block 5, all subjects made 100 movements in FF0 and with normal visual feedback of their hand position.

**Data analysis**

Positional and force data were sampled at 600Hz and then digitally filtered using a 4th order bidirectional Butterworth filter with a cut-off frequency of 15 Hz. Successful trials were selected on the basis of the following conditions: i) at movement onset, hand position was within the start circle (diameter of 2 cm), ii) initial velocity was lower than 0.01m/s (in some trials subjects anticipated the appearance of the target circle ('go-cue') before it actually appeared, leading to a movement start before the robot motors were turned on) and iii) the time between leaving the start circle and entering the target circle was between 300 and 500 ms. All successful trials per subject per block were analyzed and movements were omitted for which the absolute maximum lateral deviation was greater than the mean plus 3 times the standard deviation for that subject in that block. Kinematics were analyzed based on the last 10 successful inward and the last 10 successful outward movements in block 1 (baseline) and those of block 4.

**Musculoskeletal model**
The musculoskeletal model of the arm consisted of three rigid segments interconnected by two hinge joints representing the glenohumeral joint and elbow joint and has been described in full detail elsewhere (Kistemaker et al. 2006; Kistemaker et al. 2010; see Fig. 1C). In short, the arm was actuated by 6 Hill-type muscle units (two mono-articular shoulder and elbow muscles, and two bi-articular muscles; see Fig. 2). The implemented Hill-type muscle model consisted of a contractile element ($CE$), a series elastic element ($SE$) and a parallel elastic element ($PE$) as shown schematically in Figure 1C. Figure 1D shows schematically the musculoskeletal modeling procedure. Activation dynamics was describes the non-linear dynamical relationship between muscle stimulation ($STIM$; the only independent input to the musculoskeletal system) and active state ($q$; the relative amount of $Ca^{2+}$ bound to troponineC; see Kistemaker et al., 2005). Activation dynamics was furthermore dependent on the length of the $CE$ to account for the experimentally observed shifts in optimum $CE$ length as a function of the activation of a muscle (Kistemaker et al. 2005). Contraction dynamics relates $q$ to the muscle torques ($M$) using force-length-velocity relationship and joint angles. The lengths of the muscle-tendon complexes and moment arms were functions of the joint angles. All skeletal and muscle parameters (like maximal force, maximal contraction velocity, tendon stiffness, etc) were based on human cadaver studies and in-vivo and in-vitro (human and animal) experimental data (see Kistemaker et al. 2006; 2007; Kistemaker et al. 2005). Except for one parameter introducing discontinuity of the force-velocity relationship (see below), none of parameters were changed or attuned to this study. Please see appendix Kistemaker et al. (2006) for a sensitivity analysis of the used muscle parameters. The robot forces were modeled as a force applied to the hand using equation 1.

The musculoskeletal model was reformulated to ensure that all functions were continuous up to the first derivatives and useable for Direct Collocation (part of the optimization procedure; see later). This included the change in a single parameter that defined the difference in concentric and eccentric slope of the force-velocity relationship at zero $CE$ contraction velocity. This was originally set such that the slope of the eccentric part is twice that of the concentric part (see also van Soest et al. 1993). Such discontinuity in the derivative of the force-velocity relationship was found to be problematic for the optimal control (OC) solver and was set such that the slopes were equal. We carried out forward simulations with both slope factors for the movements investigated here and they showed no notable differences. Also, we have reformulated the force-length relationship of the tendon and parallel elastic component (without changing their
behavior) such that it is continuously differentiable. This was done by multiplying the force-length relationship of these elastic components by a sigmoid function. In the original formulation, tendon force \( F_{SE} \) was modeled as a quadratic spring (see e.g. Kistemaker et al. 2006):

\[
F_{SE} = k_{SE} \cdot \max[0,(l_{SE} - l_{SE\_0})]^2
\]

with \( l_{SE} \) the tendon length and \( l_{SE\_0} \) the tendon slack length. In the original formulation, the term \( \max[0,x] \) ensures that the force of the tendon is always zero if the length of the tendon is less than the slack length (i.e. the tendon is not allowed to push), yet is not continuously differentiable. To address this, we calculated \( F_{SE} \) by:

\[
F_{SE} = \frac{1}{1 + e^{-\beta(l_{SE} - l_{SE\_0})}} \cdot k_{SE} \cdot (l_{SE} - l_{SE\_0})^2
\]

The sigmoid function goes from 0 to 1, is 0.5 at \( l_{SE\_0} \) and has an arbitrary steep slope, set by \( \beta \). In words, the sigmoidal function is zero when \( l_{SE} \) is under its slack length and one above its slack length (apart from small region around slack length). We have similarly changed the formulation for the parallel elastic component.

**Cost functions: control level**

The most influential cost variable at the level of control is the sum of the squared muscle stimulations, also known as control effort (Diedrichsen et al. 2010; Fagg et al. 2002; van Bolhuis and Gielen 1999). Control effort was calculated by:

\[
J = \sum_{n=1}^{6} \int_0^T STIM_n(t)^2 dt
\]

The cost function is denoted as \( J \), \( T \) is the movement duration, \( STIM \) is the muscle activation and \( n \) denotes each muscle.

It has been suggested in the literature that fatigue is related to the total amount of muscle fibers activated (Crowninshield and Brand 1981) and was implemented by weighting the control effort cost by their relative maximal force (maximal force \( F_{max} \) is assumed here to have a fixed relationship with physiological cross-sectional area).
In the remainder of this article we will refer to this cost variable as control fatigue.

The last control variable investigated is called the MinMax and minimizes the maximal muscle activation (Rasmussen et al. 2001). For numerical reasons an approximation for MinMax was used (see Ackermann and van den Bogert 2010):

\[ J = \sum_{n=1}^{6} k \int_0^T \text{STIM}_n(t)^{10} \, dt \]

As STIM is the relative muscle stimulation frequency (between 0-1), setting the exponent to 10 causes the cost for MinMax to be extremely low (<10^{-10}). Rather than lowering the threshold of optimality conditions on the cost function, we used an arbitrary large number k to rescale the cost. For \( k > 1 \cdot 10^5 \) no differences in solutions were found.

Cost functions: dynamics level

At the dynamics level, three cost variables were used. First, we implemented muscle torque change (Uno et al. 1989) that minimizes the sum of squared individual muscle torques (\( M \)) differentiated with respect to time:

\[ J = \sum_{n=1}^{6} \int_0^T \left( \frac{dT_n(t)}{dt} \right)^2 \, dt \]

Second, muscle effort (or load sharing) typically assumes that the sum of squared forces produced by the individual muscles is minimal (e.g. An et al. 1984):

\[ J = \sum_{n=1}^{6} \int_0^T T_{CE,n}(t)^2 \, dt \]

Or, alternatively, they can be scaled for the maximal isometric force (\( F_{max} \)) of the individual muscles (\( F_{CE} \)) to minimize muscle fatigue (e.g. Crowninshield and Brand 1981):

\[ J = \sum_{n=1}^{6} \int_0^T \frac{F_{max,n}}{F_{max,n}} \int_0^T F_{CE,n}(t)^2 \, dt \]
Cost functions: kinematics level

At the level of kinematic cost variables, there is only one cost variable referred to in the literature and is termed jerk (Flash and Hogan 1985):

\[ J = \sum_{n=1}^{N} \int \dddot{\theta}_n^2 dt \]

In which \( \dddot{\theta}_n \) refers to joint space jerk: the third time derivative of the shoulder and elbow joint angle.

As mentioned above, in this study we used visual perturbations that influenced the curvature of the perceived kinematics. Based on the idea that the brain may integrate visual and somatosensory information to estimate hand position (e.g. van Beers et al., 1999; Smeets et al., 2006)) and hence jerk, we also investigated a cost function of weighted jerk:

\[ J = \alpha \sum_{n=1}^{N} \int \dddot{\theta}_n^2 dt + (1-\alpha) \sum_{k=x,y}^{T} \int \dddot{c}_k^2 dt \]

Here, \( \alpha \) is the relative weight factor and \( \dddot{c}_x \) and \( \dddot{c}_y \) denote the visual cartesian hand jerk. \( \dddot{c}_x \) is calculated by (see also Eq. 2):

\[ \dddot{c}_x = \frac{d^3}{dt^3} (-R \cdot \cos(\arcsin \left( \frac{c_y}{R} \right)) + x_h) \]

Note that \( c_y \) is unaffected by the visual perturbation and, as stated before, \( x_h \) is the actual hand position in the x-direction. Note also that the two terms in the cost function have different dimensions and are nonlinearly related, and thus the exact value of the relative weight is non-informative. As a first order approximation of equal weighting of the visual and somatosensory information, we first identified the \( \alpha \) for which in the unperturbed condition the two costs were equal (\( \alpha = 0.11 \)). The optimal path for (unperturbed) visual jerk of the hand is a straight line from the start to the end and as such the optimal path for this value of \( \alpha \) is about half of the curve that is typical for minimizing joint based jerk. This value was used to find the optimal paths in the experimental conditions.

There is, however, no a priori need for equal contributions. For example, one could use Bayesian optimal cue combination and allow for different visual and somatosensory
contributions. This may improve the quality of the predictions. Such a weighting requires knowledge about how the brain may combine two signals with different coordinate frames and about the relative variance of the signals (van Beers et al. 1999; van Beers et al. 2002). Experimentally estimating the relative variance goes beyond the scope of this article and we have chosen to find the optimal weighting through numerical optimization. A simple golden section search method implemented in MATLAB (fminbnd.m) was used to find the optimal value for $\alpha$ (=0.128) that minimized the root mean squared difference between the experimentally observed maximal lateral x-position of the hand and of the optimal path of the model (see also Model predictions vs Experimental data in the Results) found using the optimal control techniques described below.

Optimization

For each cost function, optimal activations were found for the six muscle-tendon units of the 2DOF musculoskeletal model for a fast arm movement, similar to the experimental task. In the experiments, successful trials were those with a 'movement time' of 400 ms (±100), defined as the time between leaving the start circle and entering the target circle. Therefore the actual movement time was a bit longer and we have heuristically set the constraint movement time of the model to 425 ms. Boundary constraints matched the experiments and were the start positions of the shoulder and elbow joint (35° and 172°), desired end positions (64° and 127°), with zero angular velocity and acceleration. Importantly, initial $CE$ length and tendon length were set such that the tendons are at their slack length (the Optimal Control solver is otherwise "intelligent" enough to choose very short $CE$ lengths at movement onset and therefore 'spring-loading' the tendons that release energy). All other initial states were set to zero. The dynamic equations of the musculoskeletal model were translated and into dynamical constraint functions and discretized on several temporal nodes termed collocation points (Direct Collocation method). Important in this process was the use of an implicit formulation of musculoskeletal dynamics (see van den Bogert et al. 2011). To identify the minimal required collocation points leading to accurate solutions of the musculoskeletal model, we carried out forward simulations of the model using a variable step-size ODE solver embedded in MATLAB (The MathWorks, Inc.), with absolute and relative tolerance set to 1e-8, and using the optimal control STIM patterns obtained using different numbers of collocation points. The dynamic constraints together with the task and
boundary constraints and the cost function, were solved simultaneously using a Sparse Non-
linear Optimal Controller (SNOPT; TOMLAB Optimization Inc, Pullman, WA). The derivatives
and second derivatives of the constraint and cost function were computed analytically using
PROPT (TOMLAB Optimization Inc). It was found that the states obtained from a forward
simulation and those obtained from SNOPT were nearly identical for 45 collocation points (on
average about one collocation point per 10ms).

To reduce computation time, we ran optimizations for each cost function with increasing
numbers of collocation points starting from 15 to the desired amount of 45. For each cost
function, the optimizer was run several times using different initial guesses. First, we used an
initial guess in which all states and inputs were set to zero. In a second set of optimization runs
we used the optimal outcome of a particular cost function and used those as an initial guess for
all other cost functions. Reassuringly, optimal solutions were found to be independent of initial
guesses tested. Two exceptions were found. First, minimizing jerk led to different optimal STIM
patterns, yet with similar kinematics. This result is however to be expected as minimizing jerk
only solves the kinematic redundancy and does not lead to a unique STIM solution (i.e. there is
an infinite number of solutions for STIM yielding identical kinematics). Second, the MinMax
criterion showed local minima depending on the initial guess. Investigating the costs of several
optimization runs showed that the costs were very similar, indicating a flat cost landscape. This
can be understood as this criterion is not sensitive to changes in the activation of muscles that
have a low activation. The optimal kinematic paths were however robust against initial guesses
and therefore we simply selected per condition the optimal solution that had the lowest cost and
discarded the rest as local minima.

RESULTS

Model predictions

We first examined the predictions with the optimal control arm model for the different cost
functions for the different levels of force field. The force field was constructed such that
participants required less force to reach the target using a rightward curved movement, instead of
the leftward curved movements observed experimentally in free space (see Kistemaker et al.
2010 for a detailed explanation of the force field). The force field was either turned off (FF=0),
set to a medium level (FF1; similar to that in Kistemaker et al. 2010) or to high (FF2). To gain more insight in the relationship between predicted paths and the FF used, we also have included two intermediate FF strengths (.33 and .66, corresponding to \( b = 50 \) and 100 Ns/m\(^2\)). Inward and outward movements were very similar, and we only show here the optimal kinematic paths for the outward movements.

Figure 2 shows an overview of the predicted movements for the various cost functions at the control, dynamic and kinematic level. A first interesting results is that the predicted movements in the FF0 conditions were very similar to each other; a slightly leftward curved hand path for right arm movements (grey lines). This finding is in agreement with the literature showing that several cost variables adequately predict the common characteristics of human arm movements in free space (e.g. Alexander 1997; Flash and Hogan 1985; Kistemaker et al. 2010; Uno et al. 1989), even though they are very different in nature. However, importantly and as argued in the Introduction, these results indicate that it is experimentally very difficult to distinguish the different cost functions from each other for movements made in free space (see also Discussion).

The predicted optimal movements in the FFs were different. Kinematics obtained by minimization of cost variables at the control level and the dynamics level were in general greatly influenced by the FF and were markedly different for the different levels of FF strength (dashed lines refer to intermediate levels of FF strengths, the solid lines were identical to those used experimentally). This is because the FF was designed such that the robot opposes the movement less for movements curved rightward. This can readily be seen in the optimal solutions for control variables that include muscle force. Also, in general less muscle activation is required for smaller forces, and hence control effort cost is smaller when a rightward movement is made. These effects are stronger with increasing FF strength: the rightward bend becomes increasingly greater with the FF strength. Only for minimizing muscle torque change, changes in optimal paths were less pronounced. This will be discussed separately in the Discussion.

In contrast, minimum jerk hand paths are not at all influenced by the force field (grey and red lines in Fig. 2 overlap completely). This can be readily understood as minimization of jerk is by definition purely minimizing a kinematic variable and so the cost function does not depend on how much muscle activation or muscle force is required. Note however that even though
kinematic paths are identical, the optimal STIM pattern changed substantially for the different strengths of the FF in order to compensate for the forces applied to the hand.

Figure 2 also shows the kinematic paths predicted by the cost function combining visual (perturbed) hand jerk and somatosensory (unperturbed) joint jerk. Optimizations were run for all experimental conditions. The movements for no visual warp were similar to that of minimizing joint jerk alone, yet were straighter. This too can be readily understood, because hand based jerk, in the absence of a visual perturbation, would predict zero jerk in x-direction and thus a straight line from start to target. The diminished curvature is thus due to the added cost on visual (Cartesian) jerk. The optimal relative weighting factor $\alpha$ (see Methods) and the value for approximately equal relative weighting of visual and somatosensory jerk were very close (.13 vs 0.11 respectively) and showed very similar results. In the remainder of the paper we will only show the results for $\alpha$ set to .13. As expected, the identified optimal hand paths were not dependent on the presence or strength of the FF. The optimal movements minimizing weighted jerk were affected by the presence of the visual perturbation: movements were such to counter the perturbation.

Experimental data

Figure 2 also shows the average of the last 10 trials in FF1 and FF2, with and without visual perturbation, for both the outward and inward movements. For reference, also plotted are the averages of the last 10 baseline movements in the first block of movements with FF0w0 (recall that all subjects started with this in block 1). One subject (in the FF2w-3 group) was removed from the data set as he was not able to meet the minimal amount of 20 successful movements per block (even in the easiest block FF0w0, for which the group average success rate was approximately 85%).

By visual inspection of experimental data in Figure 2 it can be appreciated that subjects changed their kinematics when visually perturbed to counteract the perturbation; the FF0w2 movements (blue lines) are more to the left than the baseline movements (FF0w0; grey lines; note that the red lines almost entirely overlay the grey lines). This effect was larger for a greater visual perturbation (c.f. FF0w2 and FF0w3 in left and right panel respectively). Neither the presence nor the magnitude of the FF influenced the kinematic path taken by the subjects. As mentioned before, the FF1w0 and FF2w0 (red lines) are very similar to the baseline movements.
Only in combination with the visual perturbation did the subjects in the FF change their kinematics to counter the visual perturbation. Subjects in the FF visually perturbed to the right moved more to the left (FF1w2 and FF2w3; black lines) and when visually perturbed to the left moved more to the right (FF2w-3; green lines).

The effects appear rather subtle, but as it turns out they are very consistent. The effects were in general small due to the small visual perturbation used and especially relative to the distance travelled in the y-direction. To look into more detail, we have computed the change in maximal x-deviation of the kinematic paths taken by the subjects (from now on referred to as Δx-dev). This was done by calculating per subject the maximal x-deviation subtracted by the average value for the last 10x2 movements in their baseline measurement (block 1). Figure 3A shows the Δx-dev of successful trials during block 3 and 4 binned in 10x2 (inward and outward) successful trials. The successful trials were binned starting from the last 10x2 successful trials in block 4 (bin # 20) to the first successful trials in block 3. Bin numbers 1 and 2 were omitted due to a lack of successful trials (indicating an average hit rate across block 3 and 4 of around 80%). Data points are the mean values across subjects and the error bars indicate the standard error of the mean. This figure shows that changes in x-deviation occur early in block 3 and remain rather constant until the end of block 4.

To test for reliable differences in kinematics amongst the groups, we performed a split plot (mixed-design) ANOVA on the last 10x2 successful movements in block 1 and 4 (see Fig. 3B). The ANOVA indicated a significant interaction (F(6,41) = 14.8, p < 0.0001). Post-hoc paired t-tests showed that subjects moved on average significantly 4.0(±3.3) mm (p = 0.019) and 6.8(±6.5) mm (p = 0.032) more to the left when visually perturbed to the right by 20 and 30 mm respectively (see fig. 3B; note that the error bars here indicate the 95% confidence intervals). They did not significantly change their maximal x-deviation when moving in the FF (p = .86 for FF1w0 and p = .23 for FF2w0). When moving in the FF while being visually perturbed, subjects changed their kinematics independent of the FF, but only to counter the visual perturbation. They moved significantly more to the left when visually perturbed to the right (-6.7(±2.7) mm, p < .001 for FF1w2 and -9.5(±3.1) mm, p < .001 for FF2w3) and moved significantly more to the right when visually perturbed to left (9.0(±4.8)mm, p <.01). Thus while curvature was entirely independent of the FF level, subjects changed their kinematics significantly to counteract the visual perturbation. However, subjects did not fully compensate for the distorting effect of the
warped visual feedback; on average 28%. These results are in agreement to a previous study using a similar visual distortion (Wolpert et al. 1995). Results are summarized in Table 2.

Table 2 Overview statistical results change maximal x-deviation.

<table>
<thead>
<tr>
<th></th>
<th>Δx-dev(mm)</th>
<th>std (mm)</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>FF0w2</td>
<td>-4.0</td>
<td>3.3</td>
<td>0.019</td>
</tr>
<tr>
<td>FF1w0</td>
<td>-0.2</td>
<td>3.4</td>
<td>0.856</td>
</tr>
<tr>
<td>FF1w2</td>
<td>-6.7</td>
<td>2.7</td>
<td>0.001</td>
</tr>
<tr>
<td>FF0w3</td>
<td>-6.8</td>
<td>6.5</td>
<td>0.032</td>
</tr>
<tr>
<td>FF2w0</td>
<td>-1.5</td>
<td>2.9</td>
<td>0.230</td>
</tr>
<tr>
<td>FF2w3</td>
<td>-9.5</td>
<td>3.1</td>
<td>0.000</td>
</tr>
<tr>
<td>FF2w-3</td>
<td>9.0</td>
<td>4.8</td>
<td>0.006</td>
</tr>
</tbody>
</table>

Model predictions vs Experimental data

Table 3 shows a comparison between the experimentally observed Δx-dev and those predicted for all cost functions. The optimal kinematics based on cost variables from the control and dynamics level did not match those observed experimentally; all optimal paths showed rightward curved movements that increased with the strength of FF set, whereas none of the kinematic paths of the subjects did. Only the paths predicted by the kinematic variables (jerk and weighted jerk) were in agreement with those observed experimentally.

Table 3 Comparison predicted and experimentally observed change in maximal x-deviation.

<table>
<thead>
<tr>
<th></th>
<th>Data</th>
<th>Control level</th>
<th>Dynamic level</th>
<th>Kinematic level</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Exp</td>
<td>CE</td>
<td>CF</td>
<td>MM</td>
</tr>
<tr>
<td>FF0w2</td>
<td>-4.0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>FF1w0</td>
<td>-0.2</td>
<td>35.4</td>
<td>95.4</td>
<td>51.7</td>
</tr>
<tr>
<td>FF1w2</td>
<td>-6.7</td>
<td>35.4</td>
<td>95.4</td>
<td>51.7</td>
</tr>
<tr>
<td>FF0w3</td>
<td>-6.8</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>FF2w0</td>
<td>-1.5</td>
<td>47.4</td>
<td>122.0</td>
<td>71.7</td>
</tr>
<tr>
<td>FF2w3</td>
<td>-9.5</td>
<td>47.4</td>
<td>122.0</td>
<td>71.7</td>
</tr>
<tr>
<td>FF2w-3</td>
<td>9.0</td>
<td>47.4</td>
<td>122.0</td>
<td>71.7</td>
</tr>
</tbody>
</table>

All values reported are Δx-dev in mm. Exp = experimental data; CE = Control Effort; CF = Control Fatigue; MM = MinMax; TC = Torque Change; ME = Muscle Effort; MF = Muscle Fatigue; J = Jerk and WJ = Weighted Jerk.
The subjects readily changed their kinematics when visually perturbed. Irrespective of FF magnitude, they moved in order to counteract visually perturbed movement curvature. These changes in kinematics cannot be explained by minimizing control or dynamic cost variables. When visually perturbed to the right, subjects changed their hand paths to the left, and therewith increasing the cost at the control and dynamics level. Furthermore, the visual perturbation was such that it was zero at both the start and the target position and thus muscle activation patterns do not need to be adjusted to adequately reach the target when visually perturbed (see also Wolpert et al. 1995). Also, the cost for the variables at the control level and dynamic level are not influenced by the (perceived) changes in kinematics. On the other hand, a cost function that combined visually perceived jerk and somatosensory perceived jerk was capable of adequately predicting the kinematic hand paths taken in all experimental conditions. The arrows in Figure 3B, show the predicted changes in maximal x-deviation predicted using weighted jerk. \( \alpha = .128; \) see Methods.

After showing that a cost function based on weighted jerk is capable of adequately predicting the spatial aspects of the kinematic paths, we investigated the temporal aspects comparing the velocity profiles of the model and the subjects. In Figure 4, the grand mean of the y-velocity profiles of the hand of all subjects in the last 10 movements in all experimental conditions is plotted, together with the standard deviation. The subject averages per experimental condition were aligned on instant of peak velocity to calculate the grand mean. In black the velocity profile is plotted for the optimal path for the weighted visual and somatosensory jerk. The optimal y-velocity profiles for the different experimental conditions did not change notably. The experimentally observed maximal velocity was 1.37 m/s (± .13) and was 1.38 m/s (± .00) for the model. The experimentally observed time to peak velocity (time between 1% of peak velocity and reaching peak velocity) was 0.189 s (±.018) and was 0.199 s (±0.003) for the model. Together with Figure 3B, these results show the excellent fit between experimental data and the optimal kinematic paths for weighted jerk in all conditions tested experimentally.

DISCUSSION

In this study we tested a number of hypotheses about how the brain controls voluntary arm movement. Specifically, we investigated to what extent control, dynamic and kinematic variables
play a role in movement path selection. To do so, we had 7 groups of subjects move in a novel FF at different strength levels while being visually perturbed. The visual perturbation changed the visual curvature of their hand paths. We used a detailed non-linear musculoskeletal model of the human arm in combination with Direct Collocation and a sparse non-linear optimal control solver to predict optimal movement paths using various cost variables. The first important finding was that, in line with the literature, all cost variables investigated (be it at the control, dynamic or kinematic level), were capable of adequately predicting the kinematic paths taken by subjects in free space, at least for the 2D planar tasks studied here. These results clearly show that it is problematic to discern different cost functions on the basis of movements performed in free space. The predicted movements in the FFs did show a clear change: optimal movement paths based on all control and dynamic variables were different depending the strength of the FF (see Fig. 2 and Table 3). In general, the stronger the FF, the more movements curved rightward. The predicted kinematics based on the kinematic cost variable (jerk; Flash and Hogan 1985) were not affected by the FFs. The experimental results showed that none of the subjects’ kinematics was influenced by the FF; subjects moved like they did in free space. However, when feedback was perturbed such to change the visual curvature of the hand, subjects moved more to the left when visually perturbed to the right and vice versa. They also did so irrespective of FF magnitude. The experimental results were found to be consistent only with a cost function that is solely comprised of cost variables on the kinematic level (see Fig. 3 and Table 3).

It is unlikely that the lack of adaptation of the subjects to the FF is caused by flaws in the experimental setup and/or protocol. The strength of the FFs was set such that it is implausible that the change in control and dynamic costs was below the participants’ threshold for detection. The two levels of the FFs led to an average maximal force in the y-direction of about 35 N and 46 N and subjects also reported getting tired from making movements in the FF. Furthermore, if the different paths in the FF lead only to changes in cost below their threshold, they would do so when moving in free space and would hence not play a substantial role. It is unlikely that providing visual feedback of the hand played a role in not adjusting their kinematics. The FF1w0 condition in this study was, apart from the provided visual feedback, identical to a previous study that showed similar results in the FF (Kistemaker et al. 2010). It is also unlikely that subjects did not converge to stable behavior due to lack of training. The subjects were gradually introduced to the perturbations of their condition over 100-150 movements (block 3; see Methods) and then
made twice 100 movements with the full perturbation (block 3 and 4), of which only the last 10 inward and last 10 outward movements of block 4 were used for statistical data analyses. First, as can be appreciated by Figure 3A, the changes in x-deviation did not change much from early exposure to the perturbations in block 3 to that at the end of block 4, providing further evidence that subjects' behavior is not due to a lack of training. Also, in a previous study with a similar force field (yet without visual feedback and visual perturbations) movements did not change over hours of training (Kistemaker et al. 2010). Furthermore, the subjects had a high percentage of successful movements in block 4 (~80% vs ~85% in the FF0w0 condition). Lastly, the standard errors of the mean of maximal x-deviation (i.e. the error bars in Fig. 3A) indicated no difference in difficulty when taking another path then they do in FF0. One might argue that control difficulties in the FF impede the motor system’s ability to adapt movements. The presence of visual-perturbation data dispels this concern. When visually perturbed to the left during FF learning, subjects readily change their hand paths to the right, resulting in lower cost at the control and dynamics level. When visually perturbed right, subjects readily moved more to the left and therewith increased the control and dynamical cost. However, subjects do not change their path in the FF when not visually perturbed. Lastly, the presence of local minima could have hampered subjects to adapt. However, the optimal trajectories for several intermediate strength levels of the FF show a gradual increase in curvature for the control and dynamic variables and as such do not indicate local minima. On the contrary, this result indicates a continuous negative gradient in cost that, from a pure minimization perspective, would simplify finding the optimal paths.

Our data clearly suggest that neither control cost variables nor dynamic variables play an important role in kinematic path selection. Based on the results one may argue that a possible exception would be muscle torque change: the kinematics predicted were much less affected by the FF than the other dynamic variables. The effect of the FF is less pronounced for the movements minimizing this cost, because it does not penalize the magnitude of the muscle torques, but the rate of change of the produced muscle torque. Be that as it may, muscle torque change is unlikely to play an important role in kinematic path selection. First, the optimal solutions of the control variables and dynamic variables, including torque change, are not affected by the visual perturbation (see also Wolpert et al. 1995). This is because i) at the start and target position, visual warp was zero and as such the control signals do not need to be
adjusted to adequately arrive at the target and ii) control cost and dynamic cost do not change on
the basis of (perceived) kinematics. However, subjects showed clear and significant changes in
kinematics while being visually perturbed. Second, while the predicted effects of the FF's on
torque change may be small compared to those obtained when minimizing other cost variables,
they are actually very large when compared to the experimental data: the predicted changes in x-
deviation are about 8 mm to the right for FF1 and over 22mm for FF2 versus -0.2 and -1.5mm to
the left (not significantly different from 0 (p>.8 and p>.2); see Fig. 3B and Table 3) observed
experimentally. Clearly, these predictions based on minimization of muscle torque change are
not supported by the experimental data.

The behavioral results of this study are consistent with minimization of only kinematic
cost variables. Yet, if path selection does not depend on control and/or dynamic variables why do
subjects change their kinematics when visually perturbed? There are two major sources of
information informing the brain about movement kinematics: vision and proprioception. It is
likely that the two sources of information are combined to generate an estimate of the actual limb
kinematics, for example through Bayesian maximal likelihood estimation (Kording and Wolpert
2004). In the current study, we have perturbed the visual information and hence may indeed have
caus ed a change in perceived kinematics that is partway between the visually and somatosensory
sensed limb kinematics. This explanation is in line with our experimental results. Subjects
clearly and significantly responded to the visual perturbation of perceived hand curvature, yet did
not fully compensate; on average about 28% (which is in agreement with Wolpert et al. 1995).
This was independent of the direction of the visual perturbation and the presence of the FF. To
test the idea of cue combinations, we implemented a cost function that combined visually
perceived (perturbed) and somatosensory perceived (actual) kinematics. This cost function was
not only capable of qualitatively describing the spatial hand paths taken by the subjects in all
experimental conditions, but also adequately predicted the temporal aspects like maximal
velocity and time-to-peak velocity.

The current study provides evidence that selection of movement kinematics is based
purely on kinematic variables. In this study we have used only one kinematic variable: jerk, the
third time derivative of (angular) position (Flash and Hogan 1985). Here we would like to note
that our results would likely be consistent with any other kinematic variable that adequately
predicts movements in free space. Furthermore, even though we have used optimal control to
find the optimal paths for weighted jerk and showed that they were in agreement with the
experimental data, this does not mean that the human brain necessarily uses optimal control;
obviously any process based on kinematics variables that would yield the same kinematic
planning would be consistent with our finding.

We would like to stress here that if control and dynamic costs do not play a role in
movement planning, this does not mean that movements in free space are performed
inefficiently. In fact, using a detailed optimally controlled musculoskeletal model we have shown
that the minimal jerk trajectory is very similar to those obtained for several control and dynamic
variables, like effort, fatigue and energy in free space. Furthermore, muscle activation patterns
leading to the planed movement trajectory may in fact be selected for on the basis of effort,
fatigue or energy. Such a view is consistent with recent behavioral data and oxygen consumption
measured during force-field learning. Subjects rapidly learned how to move in a FF like they do
in free space, while oxygen consumption decreased over a longer time scale (Huang et al. 2012).

A consequence of explicit movement selection is that the brain needs to generate the
required muscle activation in a separate step. Such a hierarchical view of motor control has been
suggested in work starting from the late 1900's (John Hughlings-Jackson; see York and Steinberg
2006) to more recent studies (e.g. Hollerbach 1982; Kawato et al. 1987; Rosenbaum 1983;
Saltzman 1979) and is consistent with a body of neurophysiological data (e.g. Dum and Strick
REFERENCES


Smeets JBJ, van de Dobbelsteen JJ, de Grave DJ, van Beers RJ, and Brenner E. Sensory integration does not lead to sensory calibration, PNAS, 103(49)18781-18786, 2006.


FIGURE CAPTIONS

Figure 1. A) Schematic drawing of the experimental setup. Targets were projected onto a semi-silvered mirror using a liquid crystal display monitor suspended 15 cm above the mirror (not shown). Subjects moved from the red start position to the green target position. Two seconds after reaching the target, start and target position were swapped and subjects initiated a new movement. B) Illustration of the visual perturbation using two hypothetical trajectories of the hand (black) and the perturbed hand trajectory (blue) with w set to -30 mm. If a subject were to move straight to the target, the depicted movement would be an arc from the start position (green circle) to the target position (red circle; left panel). The visual distortion was zero at the start and target position and was maximal halfway the two positions. In order to move visually straight, participants needed to make a counter arc to the right (see right panel). C) Schematic drawing of the musculoskeletal model. The implemented Hill-type muscle-tendon complex model consisted of a contractile element (CE), a series elastic element (SE) and a parallel elastic element (PE) and included activation dynamics modeling the CE length dependent Ca\textsuperscript{2+} dynamics and active state dependent force-length-velocity relationship. D) Flowchart of the musculoskeletal modeling procedure.

Figure 2 Overview of model predictions of kinematic paths under the various cost functions and experimental data. Please note the equal scaling of the x- and y-axis. Model predictions Shown are the outward optimal movements for all cost functions investigated at control, dynamic and kinematic level. Note that the predicted kinematic paths for minimizing jerk are identical for all experimental conditions. Note also that the predicted kinematic paths do not change for different FF strengths, both for jerk and weighted jerk. Thus, for example, the red and grey line overlap completely. The predicted paths are depicted for the conditions listed in the legend. Experimental data Figure 2 furthermore shows the average hand paths of outward and inward movements of last 10 trials per condition. FF0, FF1 and FF2 refer to the strength of the FF (b=0, 150 or 225Ns/m\textsuperscript{2}) and w\textsubscript{0}, w\textsubscript{2}, w\textsubscript{3} and w\textsubscript{-3} to the visual perturbation (none, 2 cm, 3 cm and -3cm). Note that the red lines almost completely overlay the gray lines.

Figure 3. A) Average changes in maximal x-deviation of the hand trajectories relative to baseline (last 10 successful inward and 10 outward movements in block 1) during block 3 and 4 for all 7 experimental conditions. Movements were binned in 20 successful (10 inward and 10 outward) movements, starting from the last 20 successful trials. The first two bins were omitted due to a lack of successful movements. Data points are the mean values and error bars indicate standard error of the mean. B) Close-up of Δx-dev in the last 10 inward and outward movements of block 4. Note that the error bars here denote the 95% confidence interval. The asterisks denote means significantly different from zero (*=<.05, **=<.01 and ***= <.001). The arrows represent the predicted changes in maximal x-deviation for the cost function using weighted visual and somatosensory perceived jerk.

Figure 4. The average velocity profile of the hand in the y-direction (fore-aft) of all subjects of the last 10 inward and 10 outward movements in all experimental conditions (grey line; the grey surface indicates the standard deviation). The optimal velocity profile predicted for the minimization of combined visual and somatosensory perceived jerk is plotted in black.
velocity profile outward

- **weighted jerk**
- **data**

**y velocity [m/s]**

**time [s]**

0 0.1 0.2 0.3 0.4 0.5 0.6