Submitted to Journal of Neurophysiology

Energy-related optimal control accounts for gravitational load: comparing shoulder, elbow and wrist rotations.

Abbreviated title: Gravity force integration in movement planning

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Abstract

We permanently deal with gravity force. Experimental evidences revealed that moving against gravity strongly differs from moving along the gravity vector. This directional asymmetry has been attributed to an optimal planning process that optimizes gravity force effects in order to minimize energy. Yet, only few studies have considered the case of vertical movements in the context of optimal control. What kind of cost is better suited to explain kinematic patterns in the vertical plane? Here, we aimed to further understand how the CNS plans and control vertical arm movements. Our reasoning was the following: if the CNS optimizes gravity mechanical effects on the moving limbs, kinematic patterns should change according to the direction and the magnitude of the gravity torque being encountered in the motion. Ten subjects carried-out single joint movements, i.e., rotation around the shoulder (whole arm), elbow (forearm) and wrist (hand) joints, in the vertical plane. Joint kinematics were analysed and compared to various theoretical optimal models predictions (minimum absolute work-jerk; jerk; torque change; variance). We found both direction-dependent and joint-dependent variations in several kinematic parameters. Notably, directional asymmetries decreased according to a proximo-distal gradient. Numerical simulations revealed that our experimental findings could be attributed to an optimal motor planning (minimum absolute work-jerk) that integrates the direction and the magnitude of gravity torque and minimizes the absolute work of forces (energy related cost) around each joint. Present results support the general idea that the CNS implements optimal solutions according to the dynamical context of the action.

Key words: sensorimotor control, reaching movement, gravity force, optimal control, proximal, distal
Introduction

We permanently interact with gravity force. How the CNS deals with the dynamic effects of gravity is an important issue in motor neuroscience. Several psychophysical studies have emphasized the preponderant role of gravity force on motor control. For instance, it has been proposed that the CNS uses an internal model of gravity acceleration to supplement sensory information when estimating time-to-contact with an approaching object (McIntyre et al. 2001). In addition, recent results on sensorimotor adaptation occurring after a space flight indicated that a misrepresentation of gravity force strongly influenced the motor planning process of arm movements (Gaveau et al. 2011).

It is appealing that the CNS plans vertical movements in a particular way: moving against gravity dramatically differs from moving along the gravity vector. Precisely, accumulative results have shown that upward movements have greater curvature, greater peak of acceleration, and shorter acceleration time than downward movements (Atkeson and Hollerbach 1985; Papaxanthis et al. 2003b; Papaxanthis et al. 1998b). Unequivocal experimental evidences argue in favour of a gravity-related origin for these particular kinematic patterns. Direction-dependent kinematic asymmetries have been observed for vertical (up versus down), but not for horizontal (left versus right) mono-articular arm movements (Gentili et al. 2007; Le Seac'h and McIntyre 2007). Kinematic asymmetries progressively attenuated during exposure to microgravity in such a way that vertical arm kinematics became symmetrical for both directions (Papaxanthis et al. 2005). Additionally, Sciutti et al. (2012) have recently shown that rightwards/leftwards horizontal arm movements became directionally asymmetric when visual feedback of movement was artificially rotated by ninety degrees. Lastly, because directional asymmetries appear very early in the movement, they likely result from feed-forward processes (Gaveau and Papaxanthis 2011).
It has been proposed that such kinematic asymmetries are the outcome of a dynamic planning process minimizing an energy-related criterion and taking into account the dynamical interaction of the body with the environment (Berret et al. 2008a). This idea, which implies that both the direction and the magnitude of gravity torque are integrated into the motor plan of arm movements, is functionally advantageous: the optimization of gravity mechanical effects (gravity torque direction and magnitude) reduces energetic costs during movement implementation. However, if the CNS optimizes arm movement dynamics in the vertical plane, kinematic patterns should change according to movement context and, therefore, asymmetric patterns should not be an invariant feature of all vertical movements. This can be simply illustrated in the context of single-joint movements. During single-joint displacements of similar direction and amplitude, gravity torque varies according to the segment involved in the motion: it decreases for whole-arm, versus forearm, versus hand movements. Therefore, as a trajectory optimal for a limb segment may be non-optimal for another limb segment, one would expect kinematic asymmetries to be modulated according to the limb segment involved in the action. Precisely, as gravity torque decreases according to a proximo-distal gradient, the directional asymmetry should decrease too.

In the present study, we intended to further understand how the CNS plans and control movements in the vertical plane. Does an optimal integration of gravity into the motor plan produce asymmetric patterns in different movement contexts? What kind of optimization costs is best suited to explain kinematic patterns in the vertical plane? Various cost functions have been used to reproduce kinematic patterns of arm movements in the context of optimal control. The resulting models can be coarsely classified as: kinematic (Ben-Itzhak and Karniel 2008; Flash and Hogan 1985), dynamic (Nakano et al. 1999; Uno et al. 1989), energy related (Berret et al. 2008a; Gaveau et al. 2011; Soechting et al. 1995) or, more loosely, effort related (Crevecoeur et al. 2009; Guigon et al. 2007; Harris and Wolpert 1998; Todorov and Jordan...
Some of them were derived in a stochastic context but for the purpose of this paper it is sufficient to stick to a deterministic context. Whilst numerous studies focused on movements performed in the horizontal plane, very few studies attempted to address the case of vertical movements, mainly using energy related or effort related cost functions. We asked ten participants to perform upward and downward single joint movements around the shoulder, elbow and wrist. Upward and downward movements allowed testing the effect of gravity torque direction, whilst movements with the different joints allowed testing the gravity torque magnitude effects. We compared the kinematic patterns between directions and joints as well as with theoretical predictions based on the optimization of four different criterions (minimum absolute work-jerk, minimum jerk, minimum torque change, minimum variance).

**Methods**

*Participants*

Ten male adults (mean age = 23.8 ± 1.8 (standard deviation, s.d.) years; mean weight = 72.6 ± 6.8 kg; mean height = 176.2 ± 7.2 cm) volunteered to participate in this study. All were right-handed (Edinburgh Handedness Inventory; Oldfield 1971), in good health, with normal or corrected to normal vision, and did not present any neurological or muscular disorders. The regional ethics committee of Burgundy (C.E.R) approved the experimental protocol, which was carried out in agreement with legal requirements and international norms (Declaration of Helsinki, 1964).

*Motor task and experimental protocol*

Participants were asked to perform single-joint movements in a parasagittal plane with either their fully-extended arm (rotation around the shoulder), their forearm (rotation around the elbow), or their hand (rotation around the wrist). We choose movements with one degree
of freedom to isolate and emphasize the mechanical effects of gravity (as in Gentili et al. 2007 and Le Seac'h and McIntyre 2007). During single-joint vertical arm movements, inertia (i.e., the distribution of the arm mass around the shoulder in a body fixed coordinate system) remains constant and thus inertial torque is related only to joint acceleration. On the contrary, gravity torque in the sagittal plane significantly changes according to the movement direction and to the joint involved in the motion. Note that during single-joint movements interaction torque may also influence motion dynamics. For example, during motion of the elbow joint, inertial interaction torques may arise at the shoulder and wrist joints because of elbow acceleration and deceleration. In the present study, we verified that interaction torque cannot account for any kinematic differences between joints and directions. First, we confirmed that joint motion was restricted to the focal joint only (see data processing below). Second, by restraining elbow and wrist joints with splints, we also confirmed that directional asymmetries at the shoulder joint are not the result of asymmetric inertial interaction torques (see control experiment A below).

Participants sat in a chair with their trunk aligned in the vertical position and supported by the back of the chair (see Fig.1A). Three targets (plastic spheres, 1cm diameter) were positioned at a distance equal to the length of each segment. The middle of the targets (initial target, IT) was horizontally aligned with the centre of rotation of each joint. The other two targets were placed at an angle of 35° upwards (UT, target) and 35° downwards (DT, target) taking as reference the horizontal line formed by the length of the segments and the IT. Before shoulder-joint movements, the arm was kept horizontal (shoulder elevation 90° and shoulder abduction 0°), the elbow was fully extended and the semi-pronated hand was aligned with the upper arm and the forearm. Before elbow movements, the upper arm was vertical (shoulder elevation 0° and shoulder abduction 0°), the elbow was flexed at 90°, and the semi-pronated hand was aligned with the forearm. Before wrist-joint movements, the upper arm was vertical...
(shoulder elevation 0° and shoulder abduction 0°), the elbow was flexed at 90°, and the palm of the hand was oriented downwards. In a preliminary study, we obtained similar results for wrist movements performed with the palm oriented upwards or downwards. Therefore, for simplicity reasons, we reported here results of hand movements with the palm oriented downwards. Note that wrist movements were not realized with the same initial position (i.e., semi-pronation) as the one used during shoulder and elbow movements. Our aim was to allow large movement amplitudes and consequently to emphasize the importance of gravity torque over the whole wrist dynamics. Flexion-extension of the wrist present smaller stiffness and larger amplitude than radio-ulnar deviations (Charles and Hogan 2012; Crisco et al. 2011; Formica et al. 2012).

From these initial positions, participants were requested to perform as fast as possible and uncorrected visually guided arm movements towards the UT and the DT. They were informed that final accuracy was not the primary goal of the task. Movements were carried out in a block-design (shoulder, elbow, and wrist), which was counterbalanced across participants. Within each block of shoulder, elbow and wrist movements, participants accomplished 24 trials (12 upwards and 12 downwards) in a random order. To prevent fatigue, blocks were separated by a 5 minutes interval. In addition, a short rest period (~ 10 s) separated each trial. The experiments were performed under normal lighting conditions.

Kinematics recording

Kinematics was recorded by means of an optoelectronic device (SMART-BTS, Milan, Italy). Five cameras (sampling frequency 120Hz) were used to record the displacements of five reflective markers (10 mm in diameter) placed on the right shoulder (acromial process), elbow (humeral lateral condyle), wrist (ulnar styloid process), hand (first metacarpophalangeal joint), and index finger (nail).
Data processing

Data processing was performed using custom Matlab programs (Mathworks, Natick, MA). Kinematic signals were low pass filtered (cut off frequency 5Hz) using a digital fifth-order Butterworth filter (zero-phase distortion, ‘butter’ and ‘filtfilt’ functions). 3D velocity signals were inspected to ensure that they were single-peaked. Angular displacements were also inspected to verify that participants performed one degree of freedom movements (< 4% of all trials) with the required joint (shoulder, elbow or wrist). Joint movements were discarded from further analysis when they presented multiple local maxima and/or a rotation (≥ 3°) to other than the requested joint.

We defined movement onset and offset with a threshold of 10% of the maximal angular velocity. Angular kinematics were then characterized by calculating the following parameters (see Fig. 1B): i) movement duration (MD), ii) amplitude of joint angular displacement, iii) peak acceleration (PA) and time to peak acceleration (tPA), iv) peak velocity (PV) and time to peak velocity (tPV), and v) peak deceleration (PD) and time to peak deceleration (tPD). From the above parameters, we calculated three invariant parameters to characterize kinematic patterns: i) relative time to peak acceleration (rtPA= time to peak acceleration/movement time), ii) relative time to peak velocity (rtPV= time to peak velocity/movement time), and iii) relative time to peak deceleration (rtPD= time to peak deceleration/movement time). The above parameters are termed invariant because they can, theoretically, remain constant across experimental conditions if the brain appropriately scales joint torques and movement speed (Atkeson and Hollerbach 1985; Hollerbach and Flash 1982). Here, they have been used as ‘tools’ to examine whether participants produce similar kinematic patterns for the different joint and direction conditions. In addition, to make qualitative comparisons between joints and directions, we normalised the velocity profiles in time (cubic spline function, Mathworks,
Natick, MA) and amplitude (velocity time series divided by maximal velocity). Normalisation guarantees that velocity profiles are independent of joint amplitude, time, and maximal velocity. Lastly, to illustrate directional differences between upward versus downward arm movements, we computed the ratio of directional asymmetry ((Down-Up)/Down*100) for the different kinematic parameters.

**Statistical analysis**

We checked that kinematic variables were normally distributed (*Shapiro-Wilk W test*) and that sphericity was respected (*Mauchley tests*). Kinematic parameters were compared by means of ANOVA, with *joint* (shoulder, elbow and wrist) and *direction* (upward and downward) as within subject factors (level of significance, P<0.05). Post-hoc differences were assessed by means of *Scheffé* tests (level of significance, P<0.05).

**Optimal movement simulations**

**Minimum absolute work-jerk model**

Previous studies have shown that minimizing mechanical energy expenditure while maximizing joint smoothness is a suitable optimization method for replicating kinematic features of vertical arm movements. This model has been described in depth in the context of direct/inverse deterministic and stochastic optimal control of single or multi-joint arms (Berret et al. 2011a; Berret et al. 2008a; Gaveau et al. 2011). In our study, we took advantage from this model to simulate shoulder, elbow and wrist movements. We used the following equations of dynamics, $\theta$ being the angle between the segment and the horizontal axis:

\[
\tau_{ag} - \tau_{ant} = I \ddot{\theta} + B \dot{\theta} + G T(\theta) \quad (1)
\]

\[
\sigma \ddot{\tau}_{ag} = \gamma u_{ag} - \tau_{ag} \quad (2)
\]
\[ \sigma \ddot{\tau}_{ant} = \gamma u_{ant} - \tau_{ant} \quad (3) \]

The first equation describes the equation of motion for a single-joint, with moment of inertia \((I)\), viscous friction coefficient \((B=0.87; \text{see Nakano et al. 1999})\), gravitational torque \((GT(\theta) = m \cdot g \cdot r \cdot \cos \theta)\), gravitational acceleration, \((g = 9.81 \text{ m.s}^{-2})\), mass of the limb \((m)\), distance between the joint’s centre of rotation, and the joint’s centre of mass \((r)\). The constant \(\gamma\) is a gain factor that scales muscle activation to joint torques \((\gamma = 100)\). The last two equations describe muscle dynamics for a pair of agonist/antagonist muscles as a first-order low-pass filter. Anthropometric parameters were adjusted for each subject based on their mass, height, and limb lengths (Winter 1990).

The control variable can be thought as the motor neuron inputs to the muscles; respectively, \(u_{ag}\) (agonist) and \(u_{ant}\) (antagonist). We add the constraint \((u_{ag}, u_{ant}) \in [0,1]^2\), which enforces the positivity of muscle activations; therefore, muscle torques are generating by emulating the “pull-only” behaviour of human muscles. The net torque acting at the shoulder joint is simply obtained by subtracting the agonist and antagonist torques \((i.e. \tau_{ag} - \tau_{ant})\).

The absolute work-jerk model relies on the following cost function:

\[ C = \int_0^{MD} \left| \tau_{ag} \dot{\theta} \right| + \left| \tau_{ant} \dot{\theta} \right| + \alpha (d\dot{\theta}/dt)^2 \, dt \quad (4) \]

where \(\alpha\) is a weighting factor to normalize the relative magnitude of the jerk term in the total cost function. Since during reaching movements the smoothness cost usually assumes values higher than the energetic cost, we chose \(\alpha = 0.004\) and kept this value constant for all simulations. We nevertheless checked that the results presented in this paper are not significantly affected by variations of this factor (ranging from 0.001 to 0.1).
The optimal control problem is then formulated in the following way: find a control vector \( \mathbf{u} = (u_{ag}, u_{ant}) \) driving the system from an initial equilibrium posture \( \theta_0 \) to a terminal equilibrium posture \( \theta_T \) in time \( MD \), while yielding a minimum cost value \( C \). This optimal control problem was solved numerically using a Gauss Pseudo-Spectral method and the open-source software GPOPS (Benson et al. 2006; Garg et al. 2009; Rao et al. 2010).

A posteriori verifications showed that the control variable was smooth and that the boundary values were not reached. We also checked that the Pontryagin's maximum principle necessary conditions were verified (such as the constancy of the Hamiltonian). This model reproduces, in a stable and robust way, the up/down asymmetries for full-extended arm movements in the vertical plane. It is important to note that these asymmetries are related to energetic considerations as it is well known that the minimum jerk, alone, always predicts symmetrical velocity profiles (Flash and Hogan 1985).

**Minimum jerk and minimum torque change models**

We performed numerical simulations for the minimum jerk (see Flash and Hogan 1985) and the minimum torque change (see Uno et al. 1989) models. We will not describe in depth these models since this was already done in numerous papers.

In the minimum jerk model, the objective function to be minimized is expressed by:

\[
C_j = \int_0^{MD} \left( \frac{d^3x}{dt^3} \right)^2 + \left( \frac{d^3y}{dt^3} \right)^2 \, dt
\]

(5)

where \( x \) and \( y \) are the time-dependent hand position coordinates.

In the minimum torque change model and minimum commanded torque change model, the objective function to be minimized is expressed by:
We derived the solution of the minimum variance model (see Harris and Wolpert 1998) in the gravity field. To simplify derivations, we assume here that the gravitational torque is constant throughout a movement, which is a reasonable assumption since gravity torque only varies slightly for the movement amplitude we considered (<18% in average, see results). In this model, motor noise affects the dynamics and noise variance is assumed to scale with the control amplitude (here we chose a factor of 20%), which is known as signal-dependent noise (Harris and Wolpert 1998). The cost to be minimized corresponds to the endpoint positional variance accumulated on some post-movement time window. In our simulations, we considered that the post-movement duration was equal to the movement duration itself. It is known that the post-movement duration may affect the symmetry ratio of the velocity profile (Tanaka et al. 2004), but here we were mainly interested in checking for the presence of directional differences (up vs down) in the endpoint velocity profiles. The minimum variance problem was solved using Matlab's `fmincon` function, using an interior-point method.

**Comparison between experimental and simulated data**

To compare the velocity profiles predicted by the different optimal criteria with those recorded experimentally, we calculated the Mean Square Error (MSE) after normalizing all velocity profiles in amplitude and duration:

\[
\text{MSE} = \frac{1}{MD} \int_0^{MD} (V_{\text{exp}} - V_{\text{opt}})^2 dt
\]

where, MD is movement duration and \(V_{\text{exp}}\) and \(V_{\text{opt}}\) are respectively the recorded experimental and simulated optimal velocities. We used two-tailed paired t-test to compare
the MSE of minimum absolute work-jerk model with the MSE of the other models. This analysis was performed for each joint and direction separately. Using the same analysis, we also compared the predicted ratio of directional asymmetry for all parameters (tPA, PA, tPV, PV, tPD) with the same ratio computed from experimental data. For both analyses, the level of significance was P<0.05.

Control Experiments

A. Shoulder rotations with elbow and wrist joints frozen

Previous studies have observed directional kinematic asymmetries for shoulder rotations in the vertical plane. These kinematic asymmetries have been attributed to gravity effects. However, because during such movements inertial interaction torque at the elbow is substantial and asymmetric, due the limited range of motion of the elbow joint, one might ask whether kinematic asymmetries couldn’t emerge from the simple influence of interaction torques. Indeed, extensor muscle activation will be required to counteract inertial interaction torques (i.e., to keep the elbow at a constant angle) during upward movement deceleration and downward movement acceleration. However, since the elbow is already maximally extended in the starting position, no reciprocal activation of flexor muscles is needed to counteract inertial interaction torques during upward movement acceleration and downward movement deceleration.

Multiple results from the literature do not corroborate this hypothesis. Le Seac’h and McIntyre (2007) asked eleven subjects to perform single joint shoulder flexion/extension and abduction/adduction in two different body positions: standing up or reclined on the side. Results showed that flexion/extension as well as abduction/adduction are asymmetric when performed in the vertical plane (flexion/extension while standing up and abduction/adduction while reclined on the side) and symmetric when performed in the horizontal plane.
While interaction torque at the elbow differed between flexion and extension (because of the elbow range of motion limits), kinematic asymmetries were only observed in the vertical plane. Also, while interaction torque at the elbow is null for both abduction and adduction, kinematics asymmetries were observed in the vertical plane but not in the horizontal plane. Additionally, experiments performed in microgravity have shown that mono-articular shoulder rotations (without restraining elbow nor wrist joints) become progressively symmetric (Gaveau et al. 2009).

Here, in order to specifically test that asymmetric inertial interaction torque at the elbow did not produce directional kinematic-asymmetries, we asked three subjects (all males; mean age = 25.3 ± 1.15 years; mean weight = 70 ± 6.2 kg; mean height = 179 ± 6.08 cm), who did not participate in the main experiment, to perform shoulder rotations, while they wore splints restraining both their elbow and wrist joints. Assuming that splints perfectly prevent joint motion at the elbow and wrist joints (the experimenters physically verified that no motion was allowed in any plane), shoulder rotations were not anymore subject to interaction torques at the distal joints (here we neglect finger interaction torques). Experimental procedures and data analysis were similar to the main experiment.

B. Elbow rotations with an additional load

Six right-handed adults (4 males; mean age = 25.2 ± 1.1 years; mean weight = 69.6 ± 4.7 kg; mean height = 171.6 ± 4.4 cm), who did not participate in the previous experiments, took part in the control experiment B. Our purpose was to examine whether an increase in the gravito-inertial torque magnitude could change the control processes at a given limb. We expected that if gravity torque is taken into account by the CNS so as to optimize movement control, increasing the gravito-inertial torque at the elbow joint should change kinematic
parameters toward those observed for the proximal shoulder joint. To this aim, subjects were required to perform elbow rotations under two different load conditions: without any additional load (NL) and with an additional load corresponding to 30% of their estimated forearm mass (L). The additional load was fixed on the center of mass of each participant’s forearm. Apparatus, instructions, recordings and data processing were similar to those of the main experiment. Because not all variables showed a normal distribution (Shapiro-Wilk W test), we performed non-parametric test (Wilcoxon). We also performed optimal simulations for the control experiment B. We used the same model as described above in the main section; we only adapted anthropometric parameters for the new subjects as well as for the additional load condition. We used the same non-parametric test (Wilcoxon) to compare simulated results between them as well as with experimental results.

C. Accounting for interaction torques with a multi-joint model

In the main study, movements were considered as single-joint due to the task instruction, and thus each limb could be represented as a single rigid body rotating around its proximal joint. However, the true mechanical problem posed to the CNS is multi-joint and also includes the control of interaction torques to maintain the position of other body parts constant. For instance, for an elbow flexion, the CNS possibly attempts to freeze the shoulder joint by counter-acting the inertial effects due to forearm rotation. In order to account for the existence of interaction torques, we tested the robustness of our theoretical results in the case of a 2-dof arm model. Note that, modelling the arm as a 3-dof system would uselessly complicate computations, since wrist movements are dominated by stiffness and gravity torque (Charles and Hogan 2011). Because our optimal control model minimizes a dynamic cost and interaction torques are acceleration-dependent and velocity-dependent, one could ask whether taking into account these interactions torques could change the model predictions.
Intuitively, since the shoulder joint does not move as it is frozen, shoulder torque will not
work and shoulder angle jerk will be zero. Thus, the overall cost should be unchanged. Yet,
only real simulations can reveal the complete optimal strategy for such 2-dof movements.
Hence, for each joint we performed new simulations with the additional constraint to stabilize
another joint.

Results

General features

Overall, all participants followed our instruction to perform movements as fast as
possible; all conditions combined, the average movement time was 0.35±0.06s (s.d).
Furthermore, although final accuracy was not the primary constraint in our experiment, all
participants performed accurate joint movements: all conditions combined, the average
amplitude was 34.19°±1.05°. ANOVA did not reveal any main or interaction effects for joint
amplitude (for all analyses, P>0.4). Fig. 1A illustrates typical joint displacements for the
upward and downward directions. The average initial gravitational torque was 14.3±1.94 N·m
for the shoulder, 5.83±0.86 N·m for the elbow, and 0.43±0.05 N·m for the wrist. In addition,
due to the symmetrical location of UT and DT with respect to the horizontal axis,
gravitational torque similarly decreased during an upward and a downward movement within
each joint. Specifically, the average decrease in gravitational torque was 2.59±0.35 N·m for
the shoulder, 1.10±0.16 N·m for the elbow, and 0.07±0.01 N·m for the wrist.

Kinematic features

All participants carried out pointing movements with single-peaked velocity profiles
(see Fig.1A and Fig.5) and equivalent times (see Fig.2A). The same was true for the peak of
deceleration (Fig. 2D), which was not affected by the different factors. ANOVA did not
reveal any main or interaction effects neither for movement time (P>0.2) nor for peak of 
deceleration (P>0.5). Other kinematics parameters, however, markedly differed across joints 
and directions:

Peak velocity (Fig. 2B). ANOVA revealed an interaction effect between joint and 
direction for PV (F_{2,18}=9.98, P<0.002). Post hoc tests revealed directional differences for the 
shoulder (P<0.001) and elbow (P=0.02) joints, but not for the wrist (P>0.9). Furthermore, PV 
of the shoulder was greater than PV of the elbow and wrist in upward direction (in all cases, 
P<0.01), whereas no differences between joints were found in downward direction (in all 
cases, P>0.5).

Peak acceleration (Fig. 2C). There was an interaction effect between joint and 
direction for PA (F_{2,18}=11.20, P<0.001). Post hoc comparisons showed significant differences 
between upward and downward directions for the shoulder (in both cases, P<0.001), but not 
for the elbow and wrist (P>0.5). In addition, PA of the shoulder was greater than PA of the 
elbow and wrist in upward direction (in all cases, P<0.01), whilst no differences between 
joints were found in downward direction (in all cases, P>0.5).

Time to peak acceleration (Fig. 3A). ANOVA showed a significant interaction effect 
between joint and direction for tPA (F_{2,18}=7.26, P=0.004). Post hoc comparisons showed 
differences between upward and downward directions for shoulder (P<0.01) and elbow 
(P<0.02) joints, but not for the wrist (P>0.8). In addition, tPA of the shoulder was shorter than 
tPA of elbow and wrist in the upward (P<0.05), but not in the downward (P>0.05) direction.

Time to peak velocity (Fig. 3B). There was also a significant interaction effect between 
joint and direction for tPV (F_{2,18}=11.54, P<0.001). Post hoc tests revealed differences 
between upward and downward directions for shoulder (P<0.01) and elbow (P<0.02) joints, 
but not for the wrist (P>0.8). In addition, tPV for the shoulder was shorter than tPV of the 
elbow and wrist in the upward (P<0.05), but not in the downward (P>0.05) direction.
Time to peak deceleration (Fig. 3C). Finally, a significant interaction effect between joint and direction was also observed for tPD (F_{2,18}=4.43, P=0.02). Post hoc tests showed differences between upward and downward directions for shoulder (P<0.01), but not for elbow and wrist (P>0.5). In addition, tPD for the shoulder was larger than those of the other joints in the downward (P<0.05), but not in the upward (P>0.05) direction.

These results clearly indicate that kinematic features of upward versus downward movements are highly dependent on the joint involved in the motion: directional asymmetries attenuate following a proximo-distal gradient. This finding can be further observed in Table 1, in which we show average values (± s.d) of the ratio of directional asymmetry for all the above kinematic parameters.

Normalised Kinematics. Normalisations confirmed that participants did not use a similar kinematic pattern to perform movements with different joints in the vertical plane. Indeed, normalised parameters showed that relative time to peak acceleration (rtPA), peak velocity (rtPV) and peak deceleration (rtPD) varied according to joint and direction (Table 1 and Fig 4). ANOVA analysis revealed a significant interaction effect between joint and direction for rtPA (F_{2,18}=9.25, P<0.002), rtPV (F_{2,18}=11.91, P<0.001) and rtPD (F_{2,18}=4.43, P=0.03). Post hoc comparisons for rtPA showed differences between upward and downward directions for shoulder (P<0.01) and elbow (P<0.02) joints, but not for the wrist (P>0.8). In addition, shoulder rtPA was shorter than rtPA of elbow and wrist in the upward (P<0.05), but not in the downward (P>0.05) direction. Post hoc tests for rtPV revealed differences between upward and downward directions for shoulder (P<0.01) and elbow (P<0.02) joints, but not for the wrist (P>0.8). In addition, shoulder rtPV was shorter than rtPA of the elbow and wrist in the upward (P<0.05), but not in the downward (P>0.05) direction. Finally, Post hoc tests for rtPD showed differences between upward and downward directions for shoulder (P<0.01), but not for elbow and wrist (P>0.5). In addition, shoulder rtPD was larger than those of the other
joints in the downward (P<0.05), but not in the upward (P>0.05) direction. These results indicate that normalised kinematic patterns also follow a proximo-distal gradient with strong direction-dependent variations (see Table 1). Qualitatively, these findings are illustrated in the Fig. 5, in which normalised velocity profiles from all trials of a participant (upper row) and normalised velocity profiles from all participants (lower row) are depicted. It can be observed that velocity profiles of upward and downward trials are well segregated at the shoulder, slightly overlap at the elbow and are completely intermixed at the wrist joint. Velocity profiles on the lower row attest that this observation was valid for all subjects.

Optimal Simulations

Fig. 6 qualitatively illustrates the velocity profiles predicted by each optimal criterion. It clearly appears that the minimum absolute work-jerk model is the only one that matches the upward versus downward kinematic asymmetries as well as their progressive attenuation according to a proximo-distal gradient. Table 2 shows the rtPV values predicted by the different models and those recorded experimentally. Minimum variance, minimum torque change and minimum jerk models predict symmetrical velocity profiles (rtPV=0.50-0.51) whatever the direction or the joint involved in the motion. Average MSE values between experimental and theoretical velocity profiles are shown in the Table 3. It is noticeable for all conditions that MSE of the minimum absolute work-jerk model is smaller than MSE of all the other models, reinforcing so the adequacy of this model to predict experimental findings. Statistical comparisons revealed that MSE of the minimum absolute work-jerk model were significantly smaller than MSE predicted by the other models (in all cases, P<0.04 and t>2.4), except for downward shoulder rotations predicted by the minimum variance model (P=0.2 and t=1.39). We also computed the ratio of directional asymmetry for each parameter (tPA, PA, tPV, PV, tPD) and compared it (two-tailed paired t-tests) between simulated and
experimental data. We did not find any differences between experimental ratios and ratios predicted by the minimum absolute work-jerk model (in all cases, $P>0.07$ and $t<2.1$). For the three other models, statistical differences (in all cases, $P<0.01$ and $t>3$) were found for $tPA$ (shoulder and elbow), $PA$ (shoulder), $tPV$ (shoulder and elbow), $PV$ (at shoulder and elbow) and $tPD$ (at shoulder).

Control Experiments

A. Shoulder rotations with elbow and wrist joints frozen

The three subjects performed point-to-point movements with single peaked velocity profiles and comparable movement times (average $= 0.40\pm0.02$s) and amplitudes (average $= 36.1^\circ\pm0.9^\circ$). It can be observed in Table 1 (last column) that directional asymmetry during shoulder motion is still present when the elbow and wrist joints are frozen; i.e., when shoulder rotations were not anymore subject to interaction torques. Specifically, we can observe negative ratios for $PA$ and $PV$ and positive ratios for $rtPA$, $rtPV$ and $rtPD$. Note that like in the main experiment, $PD$ is not asymmetric. Qualitatively, the similarity of the ratio values with those obtained in the main experiment can be appreciated by comparing the first and last columns in Table 1.

B. Elbow rotations with an additional load

All participants performed point-to-point forearm movements with single peaked velocity profiles (see Fig. 7A). In addition, movement times and amplitudes were comparable to those of the main experiment: the average time was $0.37\pm0.05$s (s.d) and the average amplitude was $35.2^\circ\pm1.1^\circ$. The additional mass significantly modified elbow kinematics. Precisely, the $rtPV$ changed from the No Load to the Load condition (see Fig. 7A), mainly for the upward movements, and therefore the ratio of directional asymmetry increased with the
added load (load: 5.7±0.8% and No load: 3.3±0.5%; Z > 2 and P < 0.003). The minimum Absolute Work-Jerk model closely matches the increase of the ratio of directional asymmetry for elbow movements in the load condition (load: 5.4±0.2% and No load: 3.1±0.3%; Z > 2 and P < 0.003; see Fig. 7B).

C. Accounting for interaction torques with a multi-joint model

Results from these additional simulations are presented in Fig. 8. First, it can be observed that frozen joints could be appropriately stabilized (third row in Fig. 8). Second, compensating for interaction torques did not impair the capacity of the model to reproduce the experimentally observed proximo-distal gradient on directional up/down asymmetries. Indeed, as predicted by the simplified biomechanical model (first and second row in Fig. 8), the optimal strategy was still to produce asymmetric velocity profiles when moving the shoulder joint, an asymmetry which decreases for the elbow joint and disappears at the wrist (fourth row in Fig. 8), independently of the postural control required for stabilizing the other limb. This is a proof-of-concept that, at least for the absolute work-jerk cost, the results would be unchanged if we used a multi-joint modelling.

Discussion

In the present study, we examined kinematic patterns of upward and downward single-joint movements (shoulder, elbow and wrist rotations) and found both joint-dependent and direction-dependent variations in several kinematic parameters. Furthermore, numerical simulations revealed that our experimental findings could be attributed to an optimal motor planning process that integrates the mechanical effects of gravity force (gravity torque direction and amplitude) and minimizes a compromise between the absolute work of forces
and the jerk. These findings suggest that the brain implements optimal solutions according to the dynamic context of the movement.

Kinematic patterns of vertical arm movements vary according to a proximo-distal gradient

Previous studies have shown that kinematic patterns in the sagittal plane vary with movement direction (Atkeson and Hollerbach 1985; Berret et al. 2008a; Manckoundia et al. 2006; Papaxanthis et al. 2003a; Papaxanthis et al. 2003b; Papaxanthis et al. 1998c). Here, we also found dissimilar kinematic patterns between upward and downward movements involving the proximal shoulder joint. Precisely, upward movements, compared to downward movements, presented greater peak accelerations and peak velocities as well as shorter times to peak acceleration, peak velocity and peak deceleration. These results expand those of previous studies on mono-articular upper-limb movements (Crevecoeur et al. 2009; Gaveau and Papaxanthis 2011; Gentili et al. 2007; Le Seac'h and McIntyre 2007; Sciutti et al. 2012) and confirm that direction with respect to gravity is an important parameter in the planning of vertical arm movements. Interestingly, we also found that many kinematic parameters varied according to a proximo-distal gradient. Most notably, kinematic asymmetries, observed at the proximal shoulder joint, were reduced at the intermediate elbow joint, and statistically disappeared at the distal wrist joint (see Table 1). This novel finding suggests that the brain generates motor plans in the vertical plane by taking into account the direction and the magnitude of gravity torque on each body segment. Three arguments support this premise. First, joint-dependent and direction-dependent variations in kinematic patterns were observed on normalised parameters (see Figs. 4 and 5), namely on parameters that should theoretically remain similar if subjects intention was to generate equivalent joint trajectories. Here, it is evident that subjects formulated motor plans with dynamic criteria, because a purely kinematic plan would be implemented by similar kinematic patterns whatever the direction.
and/or the joint involved in the motion. Second, in our study the only dynamic parameter that
could influence joint motion was gravity torque, since interaction torque was compensated
and arm inertia (i.e., the distribution of the arm mass around the joint) was constant (see also
control experiment A). Note, that the alternative hypothesis, postulating that joint-dependent
and direction-dependent variations in kinematics were due to a misestimation, and not
optimization, of gravity effects can be rejected. In such a case, we should have observed
either constant movement errors that would translate into significant difference between
upward and downward movement amplitude or feedback corrections during the movement
that would translate into velocity profiles presenting multiple peaks. Lastly, we found that
kinematic patterns of upward and downward movements differed from the beginning of the
motion (peak acceleration arises before 100ms, see Fig. 3A), observation which denotes a
feed-forward control process that takes into account the dynamic context of the action
(Gaveau and Papaxanthis 2011).

Optimal control of vertical arm movements

Several investigations have suggested that the brain acquires an internal model of
gravity force for the successful interaction of the body with the external environment
(Angelaki et al. 2004; Crevecoeur et al. 2009; Gaveau et al. 2011; Papaxanthis et al. 2005;
Pozzo et al. 1998; White et al. 2005). The direction of gravitational acceleration is certainly
one of the main features of this internal model. This information is very important when
catching falling objects or observing biological motions (Indovina et al. 2005; Le Seac'h et al.
2010; McIntyre et al. 2001; Sciutti et al. 2012; Senot et al. 2005; Senot et al. 2012; Zago et al.
2011). Interestingly, our experimental and theoretical data additionally suggest that the brain
internally represents the specific mechanical effects of gravitational acceleration on each body
segment and plans optimal movements according to the specific context of the action. The
fact that kinematic patterns vary according to the direction and the joint involved in the
motion argues in favour of an optimal dynamic motor planning.

Theoretical simulations performed with the Minimum Absolute Work-Jerk model
confirmed the optimality of the experimentally recorded kinematics. Although this cost is
composed of the absolute work of forces and the jerk, it is important to note that the energetic
cost alone (absolute work) predicts very well the direction-dependent and joint-dependent
variations in kinematic patterns at $1g$. Interestingly, the energetic cost predicts similar
kinematic patterns in the absence of gravity ($0g$) (Berret et al. 2008b), finding which further
reinforces the idea that joint-dependent and direction-dependent asymmetries are due to the
optimization of gravity torque. The kinematic (Jerk) cost in the model accounts for the well-
known smoothness feature of human movements. Minimizing hybrid costs allows to improve
theoretical predictions of various human movements (Berret et al. 2011a; b; Gielen 2009;
of gravity torque is further supported by the findings of the control experiment B: increasing
forearm mass, and therefore gravity torque, changes elbow kinematics that resemble to
shoulder kinematics (Fig.7). This result is in line with previous results (Hoffman and Strick
1993) which showed the influence of varying loads on the patterns of muscle activity. The
authors observed that muscular patterns of radial deviation were adapted to the force
requirement of the task. By changing the load applied to the wrist, the authors recorded
elbow-like, wrist-like, and eye-like muscular activity patterns. Here, we extended these
observations on kinematic patterns by showing that elbow movements can exhibit shoulder-
like kinematic patterns. Accordingly, presents results demonstrate that the dynamical context
of the task determines motion kinematics in the vertical plane. In our study, we modelled each
limb as a rigid body whilst in reality the CNS have to compensate for inertial interaction
torque at the non-focal joint. One could ask whether taking into account inertial interaction
torque could change the results of our model and consequently its ability to match the present experimental findings. To this aim, we carried-out additional simulations where the arm was modelled as a two-joint system (shoulder/elbow, elbow/shoulder and wrist/elbow) with one joint free to move and one joint restrained from motion (control experiment C). Findings from these simulations revealed that compensating for inertial interaction torque does not change the optimal solution at the moving joint presented in the Results section of the present paper.

Energy minimisation accounts for direction-dependent and joint-dependent variations in vertical arm movement kinematics

In the present work, we also tested whether three well-known optimal models, namely the minimum variance (Harris and Wolpert 1998), the minimum torque change (Uno et al. 1989) and the minimum jerk (Flash and Hogan 1985), could predict our experimental findings. These models, relevant for predicting several kinematic features of movements in the horizontal plane, failed to explain the specific direction-dependent and joint-dependent variations in kinematic patterns observed in this study. Note that this does not mean that their predictions cannot match some of the kinematic features of vertical motions. Indeed, all models almost match the joint kinematic patterns for downward movements. The major advantage of the minimum absolute work-jerk model, in comparisons to the others models, concerns motion against gravity.

The idea that the brain integrates the mechanical effects of gravity force to minimize the energetic cost of the movement is in line with previous studies that have acknowledged that the brain takes into account musculo-skeletal (Gottlieb 1996; Gribble and Ostry 1999; Hirashima et al. 2007; Pigeon et al. 2003; Sainburg et al. 1999) and environmental dynamics (Ahmed et al. 2008; Conditt et al. 1997; Shadmehr and Mussa-Ivaldi 1994) to appropriately plan and control arm movements. Our experimental findings support the optimal control
theory (Izawa et al. 2008; Todorov 2004; Todorov and Jordan 2002; Wolpert and Ghahramani 2000). We showed that an optimal solution (minimum absolute work-jerk model) that integrates gravity torques and minimizes the absolute work on each joint, predicts both joint-dependent and direction-dependent kinematic features when moving with or against gravity. Minimizing an energy related cost had already been successfully employed to predict reaching kinematics in the vertical plane (Berret et al. 2011b; Gaveau et al. 2011; Soechting et al. 1995). In addition, by directly measuring the metabolic power, Huang et al. (2012) have demonstrated that the CNS truly re-optimizes arm movements by decreasing an energy related cost when learning to reach in a new dynamical environment. Whilst energy appears to be an important criterion in movement production, it has been shown that, depending on motion context, motor planning can reflect the integration of various objective functions, related to kinematics and dynamics. For example, within the framework of optimal feedback control, Mistry et al. (2013) have recently suggested that including kinematic constraints into the motor plan helps the brain dealing with environmental uncertainty. It has been proposed that moving along straight paths is an important kinematic criterion during motor adaptation to a new environment (Kistemaker et al. 2010; Wolpert et al. 1995). In this way, experimental findings that appear contradictory at first glance, such as kinematic versus dynamic motor planning, could be reunified under the prism of optimal control theory.

Learning optimal control strategies is an important process in motor control because we permanently interact with unstable and changing environments. As an optimal behaviour in one context is no more optimal in a new one (Diedrichsen 2007; Emken et al. 2007), motor adaptation must rapidly drives to new optimal motor patterns (Crevecoeur et al. 2009; Gaveau et al. 2011; Izawa et al. 2008). Findings from microgravity experiments support this idea. After sufficient exposure to weightlessness, subjects develop new motor strategies (Bringoux et al. 2012; Papaxanthis et al. 2005; Papaxanthis et al. 1998a); as a consequence, re-adaptation
to normal-gravity conditions is necessary (Gaveau et al. 2011). Sometimes, however, suboptimal behaviours are observed. Indeed, two studies have reported results suggesting that the gravity force internal representation can lead to suboptimal control (Sciutti et al. 2012; Senot et al. 2005). Both studies used virtual reality system providing the subjects with non-biological feedback. In one study the visual feedback of the pointing movements was rotated by ninety degrees (Sciutti et al. 2012) and in the other study the subjects observed free falling objects that did not respect the rules of physics (Senot et al. 2005). In both cases, the behaviour was strongly biased by the visual feedback of the movement direction irrespectively of the real dynamics being encountered (the real torques acting on the arm and the real acceleration of the ball to catch). These studies confirm the importance of visual information for the integration of gravity force into motor planning. Whilst these results could support the idea that only the direction of gravity force is specified in movement planning, present results suggest that, when no sensorial conflict is experienced, the magnitude of the gravity torque is also specified into the motor plan.

In synopsis, we found evidence that the CNS implements optimal motor plans which integrates both the direction and the magnitude of the gravity torque on each body segment. More generally, the present results emphasize the importance of dynamics, which override kinematics, when moving in the vertical plane. The optimal interaction of the body with the external environment may be crucial for adapted motor behaviours in several species. Hooper et al. (2009) have proposed that a scaling rule, based on body (limb) size, may explain some differences in the control strategies observed across species. Large animals could devote more neural resources to the control of movement than small animals, since gravity and inertial torques increase with body size. Small animals should rely more predominantly on passive
muscle properties, since the ratio of articulation stiffness to external torques dramatically increases when animal size decreases (Hooper 2012).
This work was supported by the Institut National de la Sante et de la Recherche Medicale (INSERM). Jérémie Gaveau was supported by grants from the ministere de l'Education Nationale, de l'Enseignement et de la Recherche and by National Institutes of Health Grant R21 NS075944-02.
Disclosure

No conflicts of interest, financial or otherwise, are declared by the authors.


Figure captions

Fig. 1. (A) Initial position of participant's shoulder, elbow and wrist joints. Subject performed as fast as possible one degree of freedom pointing movements between targets in the vertical plane. Typical hand paths as well as joint paths and velocity profiles are depicted for upward (black) and downward (grey) movements. (B) Illustration of the kinematic analysis. JA, joint amplitude; PA, peak acceleration; PD, peak deceleration; tPA, time to peak acceleration; tPV, time to peak velocity; tPD, time to peak deceleration; PV, peak velocity; MD, Movement duration.

Fig. 2. Time and amplitude parameters. Average values (± s.d.) are presented for upward and downward movements performed with the shoulder (Sh), elbow (El), and wrist (Wr). (A) Movement duration. (B) Peak velocity. (C) Peak acceleration. (D) Peak deceleration. Vertical arrows indicate movement direction. Diamonds indicate significant differences between upward and downward directions. Stars indicate significant differences between joints.

Fig. 3. Non-normalised temporal parameters. Average values (± s.d) are presented for upward and downward movements performed with the shoulder (Sh), elbow (El), and wrist (Wr). (A) Time to peak acceleration. (B) Time to peak velocity. (C) Time to peak deceleration. Vertical arrows indicate movement direction. Diamonds indicate significant differences between upward and downward directions. Stars indicate significant differences between joints.

Fig. 4. Normalised temporal parameters. Average values are depicted for upward (U) and downward (D) movements and reveal the temporal strategy of movements performed with the shoulder (Sh), elbow (El), and wrist (Wr). For conventions see Table 1.
Fig. 5. Normalised experimental velocity profiles. Typical velocity profiles (normalised in amplitude and direction) from one participant are shown on the upper row. Average-normalised velocity profiles are shown on the bottom row. Arrows indicate movement direction.

Fig. 6. Normalised theoretical velocity profiles. Average-normalised velocity profiles predicted by the minimum absolute work-jerk (first row), minimum variance (second row), minimum torque change (third row) and minimum jerk (last row) are presented for the shoulder (Sh), elbow (El) and wrist (Wr). Arrows indicate movement direction.

Fig. 7. Control experiment B. Average relative time to peak velocity (rTPV) for experimental and simulated data and for the Load and no Load conditions are depicted. (A) Experimental average-normalised velocity profiles. (B) Simulated average-normalised velocity profiles. Arrows indicate movement direction.

Fig. 8. Control simulations (see control experiment C). Predicted angular displacement and velocity profiles are plotted against time for the single joint model (respectively first and second rows) and the two degrees of freedom model (respectively third and fourth rows). Each graph contains upward and downward simulations. Each column presents simulation for one moving joint.

Table 1. Average ratio (± s.d) of directional asymmetry for the main experiment (first three rows) and the control experiment A (last row). rtPA, relative time to peak acceleration; rtPV, relative time to peak velocity; rtPD, relative time to peak deceleration. Other abbreviations as in Fig. 1.
Table 2. Average values of the relative time to peak velocity (rtPV). rtPV values recorded experimentally and those predicted by the four models are listed for comparison.

Table 3. Average values of mean square error (MSE) calculated between simulated and experimental velocity profiles. The last column shows average MSE for each model across all experimental conditions.
A. Initial joint positions and typical Kinematic data

Shoulder joint  Elbow joint  Wrist joint

B. Kinematic Analysis

Figure 1
Figure 2

- Peak Acceleration (°/s²)
- Peak Velocity (°/s)
- Peak Deceleration (°/s²)

- Sh        El        Wr
- Sh        El        Wr
- Sh        El        Wr

- Duration (s)

A

B

C

D
Figure 3

A: Sh, El, Wr

B: Sh, El, Wr

C: Sh, El, Wr

Time PA (s)

Time PV (s)

Time PD (s)
Shoulder Elbow Wrist

Normalised Amplitude

Normalised Duration

Figure 5
Minimum Absolute Work + Jerk

Minimum Variance

Minimum Torque change

Minimum Jerk

Normalised Duration
Figure 7

Experimental

rtPV=0.46
rtPV=0.49

rtPV=0.47
rtPV=0.49

Min Abs Work + Jerk

B

rtPV=0.46
rtPV=0.48

rtPV=0.47
rtPV=0.48

Load

No Load

Figure 7
Figure 8
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<tr>
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<td>Shoulder</td>
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<td>PA</td>
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Table 1
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Table 2
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Table 3