

Title: A Modelling Perspective on the Role of Biomechanics on Motor Decision-Making

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Abstract

Recent work has shown that human subjects are able to predict the biomechanical ease and the cost of controlling the endpoint stability of potential reaching movements and to use these predictions to influence their choices between reaching movements. Here we review related experimental results in which human subjects made free choices between two potential reaching movements that varied in terms of path distance, biomechanical cost, aiming accuracy and stopping requirement, and offer a brief perspective on a potential modeling approach that would explain these results. Our main results demonstrates that prior to movement onset, control constraints such as stopping and aiming do participate in a remarkably adaptive and flexible action selection process that trades-off the advantage of moving along directions of low biomechanical cost for unconstrained movements against exploiting biomechanical anisotropies to facilitate control of endpoint stability whenever the movement constraints require it. This reveals that rather than making choices based on a minimal energy cost, the nervous system can predict additional factors, other than energy or purely abstract criteria, which may influence the decision-making process, and supports a highly context-dependent view of this process, in which the subjective desirability of potential actions may be influenced by their dynamical properties in relation to the intrinsic properties of the motor apparatus.

INTRODUCTION

For a tennis player to return the ball across the net, he can select either a forehand or backhand stroke, and the game will go on regardless of the choice made as long as the ball lands in bounds. However, the ease of the action and its reliability vary a great deal depending on one's abilities and their placement on the court. A good tennis player should use information about the structure of the motor apparatus as a function of their current posture and overall skill to quickly decide the manner to return the ball to the opposing court. Although this may sound straightforward, the implication of the arm's biomechanical aspects in the control of reaching movements has been a matter of considerable debate (Sabes and Jordan, 1997; Sabes et al., 1998; Ostry and Feldman, 2003; Krakauer and Shadmehr, 2007; Shadmehr and Krakauer, 2008; Friston, 2011). Beyond their implication in control, biomechanics must also be a factor in the selection of motor responses. To investigate this matter, we performed two experimental studies. First, we showed that some aspects of biomechanics were predicted prior to movement onset and influenced the selection between two potential reaching movements (Cos et al., 2011). In particular, subjects were more likely to select a movement trajectory aligned with the direction of maximal mobility even if it traversed a longer distance than an alternate movement. Secondly, we performed a second series of experiments aimed at investigating the effect of control constraints by varying the imposed precision and the requirement of stopping at the target across trials. We performed a comparative analysis of the subjects' free choices between movements that differed in path distance and biomechanical costs, using the basics of the experimental set-up described in (Cos et al.,

2012). Specifically, the subjects' choices varied as a function of the required control constraints, suggesting that there is a multiplicity of factors which may be predicted prior to movement onset and influence the selection of a movement.

The implication of intrinsic factors of the motor apparatus on the preparation and selection of motor actions naturally leads to the questions of how these elements may be included into a model capable of describing these processes, how these factors interact and the conditions in which this happens. Below we review some of the experimental results and the conclusions derived for an eventual computational model.

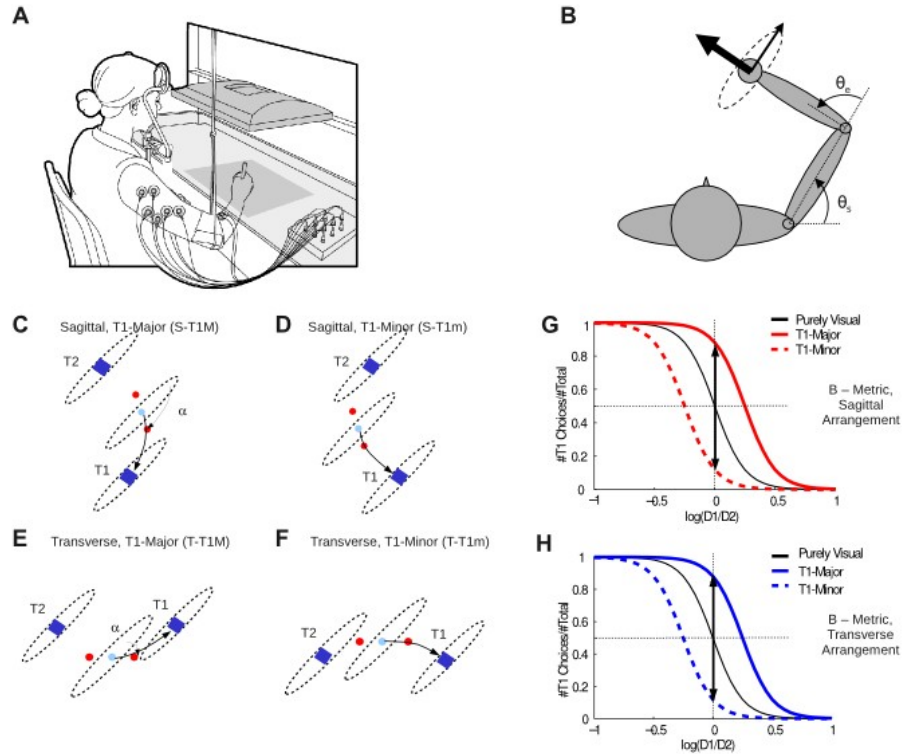


Figure 1. Experimental paradigm. **A.** Subject seated at the apparatus with her head in a chin rest and elbow in a sling that suspends the forearm approximately parallel to the digitizer surface. **B.** Definition of joint angles and the mobility/admittance ellipse at the hand (dashed line). The thick arrow depicts the large force required to accelerate the hand away and to the left, while the thin arrow depicts a smaller force required to produce the same acceleration away and to the right. **C-F.** The four arrangements of targets (blue dots), and via-points (red dots) with respect to the starting circle (cyan dot). Dashed lines depict mobility ellipses at the origin and end of movements. Arrows show example trajectories to target T1. Note that in the T1-Major arrangements, the trajectory arrives at T1 along the major axis of the mobility ellipse, whereas for T1-minor it arrives along the minor axis. **G.** Predicted choice patterns for the sagittal stimulus arrangements (C,D). The x-axis is the log of the ratio of path distances (D) to T1 versus T2, and the y-axis is the % of choices made to T1. If subjects prefer to arrive along the major axis of the mobility ellipse then the choice function for the T1-Major arrangement (solid line) should be shifted to the right of the choice function for T1-minor arrangement. If subjects do not take biomechanics into account then the choice functions should be identical (black line). **H.** Predictions for the transverse arrangements (E,F), same format. The B - Metric is the vertical distance between T1M and T1m preference curves for the case of equal relative distance.

MATERIALS AND METHODS

Characterization of biomechanics

There is a variety of biomechanical factors associated with any given movement, including passive inertia, interaction torques, muscle visco-elastic properties or more elaborated factors depending on joint kinematics and dynamics, such as muscle energy. Because our primary interest here was on how these properties affect the ease of producing and controlling arm movements in different directions, we used an approximation of biomechanics based on *endpoint mobility* and *admittance* (Hogan, 1985a, 1985b, 1985c). Endpoint mobility depends on joint configuration and captures the spatial anisotropies that result from the structure of the arm and its distribution of mass. Admittance captures the anisotropies resulting from the visco-elastic properties of the arm. As normal dynamics are never altered, we have assumed that the anisotropies of mobility and admittance will be approximately the same in the region of planar space in front of the subject, as these two metrics significantly co-vary. Mobility on the plane may be mathematically expressed as a 2x2 tensor matrix

and may be visually represented as an ellipse whose major/minor axes indicate the directions of maximal/minimal sensitivity to perturbations. Likewise, admittance may also be expressed as a 2x2 tensor and represented as an ellipse whose axes indicate the directions of maximal/minimal sensitivity. The covariance between both metrics means that the axes of both ellipses will approximately align. Based on this, we have explicitly used the *alignment of the endpoint trajectory with the major or minor axis of the mobility ellipse* as our metric of biomechanical ease, please refer to Cos et al (2011) for a thorough description of its calculation.

Behavioural Task

The task involved making free choices between two potential reaching movements, each defined with a via-point and target (see figure 1C-F). The via-points and targets were placed such that each movement was curved, with the final part of the trajectory aligned with either the major (T1-Major, T1M arrangement) or minor axis (T1-minor, T1m arrangement) of the arm's mobility ellipse (see figure 1C-F). Furthermore, the total path length between targets was varied such that the two trajectories were either the same length (11cm) or different lengths (10 vs. 12cm, or 9 vs. 13cm). In separate blocks, two other factors were also manipulated, both concerned with the control of the endpoint (see figure 3A-D, left). The first was the *aiming accuracy*, parametrized as a function of the width of the target (1 or 3cm). The other factor was the constraint of *stopping*, implemented by instructing the subject to stop at the target or to punch through it and to stop whenever afterwards. Each combination of these two constraints was performed in separate blocks, labeled as Unconstrained (U), Stopping Only (S), Aiming Only (A) and Aiming+Stopping (AS), see figure 3 (left pictures).

Each experimental session was divided into four blocks of 320 trials, each enforcing one of the four constraint conditions. Within each block, trials were of two different kinds: two-target (300) and one-target (20). The sequence of trials was generated at random and was the same in all sessions. Within each trial, each potential trajectory was defined by the origin cue (cyan dot, Radius 1cm), a via-point (red dot, Radius 1cm), and a target (dark blue square, side from 1cm to 3cm, depth 1cm, see figure 1C-F). Each trial began when the origin cue was shown on the screen and the subject placed the stylus into it. After a 300-700ms Center Hold Time (CHT), the stimuli defining one or two potential trajectories were shown. After an additional 500-700ms Observation Time (OT), a GO signal was given (origin cue disappeared). Subjects were instructed to react as fast as possible, to choose the action that felt most comfortable, and to move the stylus over the via-point and towards the target. Furthermore, the color of the via-point and target cues changed to green as the stylus slid over them. For additional control conditions, see (Cos et al., 2011).

In order to investigate the modulatory effect of control constraints, we first assessed the subject's target preference in a set of geometrical arrangements varying in path distance and biomechanics at the target. Arrangements may assume one of *two orientations*: *sagittal* or *transverse* (see fig 1C-D vs 1E-F), depending on whether the movement options are, on the horizontal plane, either away or towards the subject's body, or towards the right or left of the origin. Furthermore, arrangements may assume one of *two biomechanical configurations*: *T1 Major* (T1M) or *T1 Minor* (T1m), depending on whether the path approaching target 1 is approximately aligned with either the major or minor axis of the arm's mobility/admittance ellipses. Furthermore, in order to test the effect of the aiming and stopping requirements, we adapted the experimental set-up described in Cos et al. (2011) to accommodate the requirement of stopping and/or aiming at the target by defining four types of trials: Unconstrained (U), Stopping Only (S), Aiming Only (A) and Aiming+Stopping (AS), as shown in figure 2A-D. Figure 2A shows the baseline condition (Unconstrained, U), in which the subject is not required to stop at the target and the width of the target is three times larger than its depth. Figure 2B shows the Stopping Only (S) condition, in which the target is wide, relaxing the requirement of aiming accuracy, but the subject was instructed to stop within it. Figure 2C shows the Aiming Only (A) condition, in which the aiming requirement was enforced by the narrow width of the target, but the subject was not required to stop within it. Finally, figure 2D shows the (Aiming+Stopping, AS) condition, in which careful aiming was enforced by the small width of the target and the subject was instructed to stop within the target.

RESULTS

Choice preferences

To assess the effect of the aiming and stopping constraints on the subjects' preferences, we calculated preference curves for target 1 at each of the four geometrical arrangements (S-T1M, S-T1m, T-T1M, T-T1m - see figure 1C-F), and under each of the four constraint conditions: Unconstrained (U), Stopping Only (S), Aiming Only (A), and Aiming and Stopping (AS)

(see figure 2A-D). The preference curves, calculated by collapsing the choices across all subjects for each target and relative distance, are shown for each condition in figure 3A-D. In each of these, there is a significant influence of path distance on the target chosen, with T1 selected more often when that target is the closer of the two. Furthermore, T1 preference curves exhibit a significant shift between T1-Major and T1-Minor arrangements, thus demonstrating that the biomechanical difference between the movements exerts a significant influence on target choices. Typically, the curve for the T1-Major condition is shifted to the right of the curve for the T1-Minor condition ($p < 0.05$, bootstrap test), indicating that in the T1-Major arrangement, T1 is more appealing than T2 even when its distance from the origin is larger. This difference in target preference is a function of the path trajectory alignment, i.e., the effect of biomechanics.

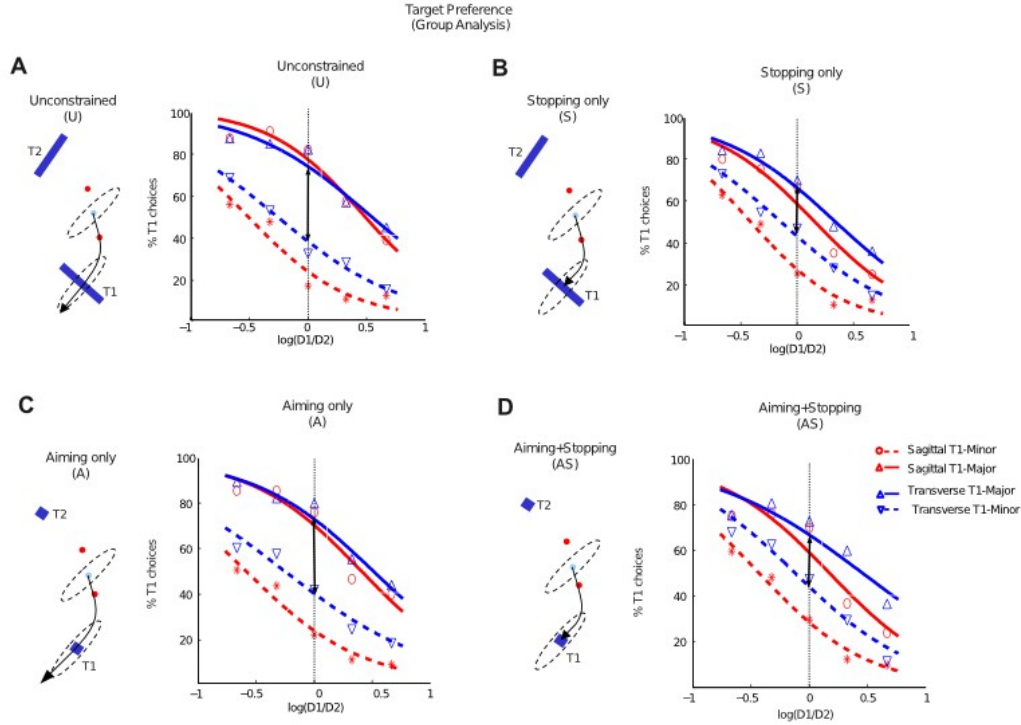


Figure 2. Group analysis of T1 preference curves for each control condition (Unconstrained U, Stopping Only S, Aiming Only A, Aiming and Stopping AS) — see depictions on top of the preference curves. **A.** Unconstrained (U) or baseline case. **B.** Stopping only (S) case. **C.** Aiming only (A) case. **D.** Aiming + Stopping case (AS). The raw data dots (symbols, see key) are fitted with sigmoidal curves for T1M (solid) and T1m (dashed) in the sagittal (red) and transverse (blue) arrangements. Note that in all cases the T1-Major curve (solid) is to the right of the T1-minor curve (dashed), showing that the T1 target is chosen more frequently in its “Major” configuration in each experimental condition and geometrical arrangement. Furthermore, a first observation indicates that the requirement of stopping at the target diminishes the effect of bio-mechanics between targets, thus the distance between solid and dashed sigmoids is shorter in those conditions in which stopping is enforced (S, AS) than in those in which the stopping requirement is relaxed (U, A) — ($B_U > B_S > B_A$).

Furthermore, a first analysis across control constraints (see figure 3) reveals that the effect of biomechanics between T1M and T1m arrangements diminishes as more constraints are gradually imposed to control the endpoint. Figure 3 shows that the influence of biomechanical ease is largest for the Unconstrained (U) condition. However, as we reduce the width of the target and enforce the requirement of aiming (Aiming Only (A) case), the B-metric diminishes only a little, indicating that aiming does not strongly modulate the effect of biomechanics. In contrast, in the Stopping Only (S) case, the B-metric is considerably reduced with respect to the A and U cases, suggesting that the requirement of stopping does exert a strong modulation of the effect of biomechanics. Supporting this is the observation that the B-metric between the S case and the AS case, in which both aiming and stopping are required, is very similar in both orientations. To summarize, the requirement of stopping substantially reduces the subjects' preference for the major target at all distances for both arrangements. In conclusion, although the control constraint conditions studied here do not invert the target preferences of subjects, the absence of on-axis control, due to the absence of a stopping requirement, increases the biomechanical ease and therefore the appeal of the targets approached along the major axis of the mobility ellipse. Overall, this first analysis suggests that the requirement of stopping reduces the effect of arm biomechanics on the decision-making process.

DISCUSSION

Decisions between concrete motor actions, such as turn right vs. turn left, have dominated animal behavior far longer than abstract decisions such as the selection of a given investment portfolio or the choice of one's career. Consequently, the demands of motor decision tasks have presumably had a more fundamental influence over the evolution of brain mechanisms than the abstract decisions usually studied in psychology and cognitive neuroscience. These demands include taking into account the biomechanical properties of the movements themselves, as these bear upon the cost-benefit of a particular choice as well as its likelihood of success. With this view in mind, this paper has analyzed how certain aspects of actions, such as biomechanical ease and controllability, influence human reaching choices.

Our experiments showed that biomechanical properties of candidate actions strongly influence the decision between them, and that this influence is modulated as a function of task constraints. Specifically, we showed that choices between unconstrained movements were strongly biased by biomechanics, but that this bias was reduced by additional constraints such as precise aiming or stopping at the target. The largest biomechanical effect (the largest shift between the T1M and T1m preference curves) was observed in the most unconstrained case (U condition). This is consistent with the endpoint moving along the direction of maximal mobility being less energy demanding and the easiest to direct. However, this may make stopping more difficult, reducing the desirability of the Major target and increasing the need for precise control. In a similar fashion, although to a much lesser extent, the aiming constraint also tends to reduce the effect of biomechanics. In conclusion, constraints of control parallel and perpendicular to the direction of movement (stopping and aiming) reduce the bias against Minor targets, where stopping is easier. One potential explanation for this is that as additional terms enter into the total cost function, the relative role of biomechanics in biasing the decision is progressively reduced.

In summary, our results reveal that biomechanics exerts a remarkable influence on target choice and that the requirement of a controlled stop at the target reduces the target preference resulting from the anisotropies of arm biomechanics. Overall, this suggests that, in addition to a hierarchy of strategies for the control of movement, there is also a multiplicity of factors which may be predicted and can influence the selection of a movement.

A modelling perspective

There is no shortage of modeling studies in the motor control community, aiming at describing how movement is generated and executed. However, most of this work is in the context of the optimal feedback control hypothesis (Todorov and Jordan, 2002), which claims movement to be continuously tuned via online feedback. By contrast, the sum of experimental results and kinematic characterization of the choice between reaching movements across conditions of different visual, biomechanical, and control cost, have highlighted that aspects related to the motor apparatus are taken into consideration during movement preparation to make decisions. In other words, the evidence presented here suggests that, if this biomechanical cost participates of the process of decision-making, it should also be included into the initial motor command sent down to the spinal cord to generate movement. By contrast, recent experimental evidence has highlighted that a remarkable minimum of six hundred ms is necessary for subjects to make decisions informed about the biomechanical cost of both potential reaching movements (Cos and Cisek, 2012). This leads us to question whether the same inverse model necessary to calculate the biomechanical cost for making decisions is used to encode the motor commands prior to movement onset.

The implication of these constraints calls for an interpretation of decision-making of motor actions with consideration to the possibility of combining forward and feedback control in a parsimonious manner. Although there is a number of models in favour of trajectory specification prior to movement onset, as suggested by a number of forward models (minimum jerk, minimum torque, minimum energy), we suggest a model that supports a minimal specification of motor commands that take into consideration biomechanical and controllability factors as a function of task demands, to be specified in the form of motor commands and to be fine tuned as the movement progresses. We believe this is an opportunity to extend existing models of decision-making and motor control to suggest possible answers to these questions.

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