

The modulatory influence of end-point controllability on decisions between actions

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Cos I, Medleg F, Cisek P. The modulatory influence of end-point controllability on decisions between actions. *J Neurophysiol* 108: 1764–1780, 2012. First published July 5, 2012; doi:10.1152/jn.00081.2012.—Recent work has shown that human subjects are able to predict the biomechanical ease of potential reaching movements and use these predictions to influence their choices. Here, we examined how reach decisions are influenced by specific biomechanical factors related to the control of end-point stability, such as aiming accuracy or stopping control. Human subjects made free choices between two potential reaching movements that varied in terms of path distance and biomechanical cost in four separate blocks that additionally varied two constraints: the width of the targets (narrow or wide) and the requirement of stopping in them. When movements were unconstrained (very wide targets and no requirement of stopping), subjects' choices were strongly biased toward directions aligned with the direction of maximal mobility. However, as the movements became progressively constrained, factors related to the control of the end point gained relevance, thus reducing this bias. This demonstrates that, before movement onset, constraints such as stopping and aiming participate in a remarkably adaptive and flexible action selection process that trades off the advantage of moving along directions of maximal mobility for unconstrained movements against exploiting biomechanical anisotropies to facilitate control of end-point stability whenever the movement constraints require it. These results support a view of decision making between motor actions as a highly context-dependent gradual process in which the subjective desirability of potential actions is influenced by their dynamic properties in relation to the intrinsic properties of the motor apparatus.

response selection; motor intention; motor control; arm; human

TO RETURN A TENNIS BALL across the net, a player 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 must use information about the structure of the motor apparatus as a function of their current posture to quickly decide to hit the ball using their backhand or their forehand, in addition to using kinematic information. 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. In

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a recent study (Cos et al. 2011), we showed that some aspects of biomechanics were predicted before movement onset and influenced the selection between two potential reaching movements. 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. However, our results did not reveal which specific biomechanical factors were responsible for this bias. Did subjects choose that movement to minimize the energetic cost? Did they choose it because it was more stable? Were these factors evaluated before movement onset?

Several pieces of evidence support the implication of biomechanical factors in the neural control of reaching movements. First, it has been observed that when reaching around pointy obstacles, trajectories are planned and executed to minimize collisions, taking into account both the passive and active resistance to potential perturbations (Sabes and Jordan 1997; Sabes et al. 1998). Second, it has been shown that the absence of visual feedback magnifies the influence of biomechanical anisotropies on motor responses (Ghez and Gordon 1987; Flanagan and Wing 1997; Flanagan et al. 2003) from the beginning of the movement. If this is the case, then some biomechanical characteristics of the arm must be taken into account in the efferent motor command (Wolpert et al. 1995; Flanagan and Lolley 2001). Third, the descending motor command from the primary motor cortex is sensitive to many aspects of biomechanics (Evarts 1968; Sergio et al. 2005; Kurtzer et al. 2006), including the interaction torques that result from intersegmental dynamics (Gritsenko et al. 2011). The leading joint hypothesis (Dounskaia 2005; Goble et al. 2007) formalized an overall control strategy that minimizes muscle effort by exploiting interaction torques, resulting in a significant bias of free reaching movements toward those directions along which the net muscle torques of the leading joint were minimal (Dounskaia et al. 2011). Fourth, anticipatory posture adjustments to facilitate subsequent movements have been observed (Morasso and Sanguineti 2002; Bottaro et al. 2008). These adjustments are presumably aimed to modify the muscular-skeletal initial conditions to facilitate subsequent movements (Lakie et al. 2003; Lakie and Loram 2006), suggesting the operation of a preliminary feedforward control strategy including at least some elements of biomechanics. Fifth, additional evidence shows that indirect factors dependent on arm biomechanics, such as muscle energy and signal-dependent noise, exert an influence on reaching movements (Harris and Wolpert 1998; Hamilton and Wolpert 2002), during both planning (Churchland et al. 2006) as well as execution (Harris and Wolpert 1998). Finally, it has been

shown that all other factors being equal, subjects' choices depended on the biomechanical costs of the movements (Cos et al. 2011). Not only does this indicate that biomechanics influence movement choices, but also that at least some aspects of biomechanics are predicted before movement onset, as the decision is being made.

The implication of intrinsic factors of the motor apparatus on the preparation and selection of motor actions naturally leads to the questions of which elements are involved, how they interact, the extent to which they exert an influence, and the conditions in which this happens. Different levels of control may be applied as a function of the task constraints and demands. For example, the level of control of mechanical impedance depends on the nature of the movement and required accuracy (Selen et al. 2005, 2006) and on additional task constraints (Gomi and Osu 1998; Trommershäuser et al. 2003). In a similar fashion, in the present study, we hypothesized that subjects' choices are influenced by arm biomechanics and modulated as a function of the control constraints demanded by the task. In other words, the selection of the movement should reflect a trade off between the influence of the predicted end-point stability and the effort associated with the movement. To test this, we investigated the effect of control constraints by varying the required precision and requirement of stopping at the target in each trial. We performed a comparative analysis of subjects' free choices between movements that differed in path distance and biomechanical costs, using the basics of the experimental setup described in Cos et al. (2011). Specifically, subjects' choices varied as a function of the required control constraints, suggesting that there is a multiplicity of factors that may be predicted before movement onset and influence the selection of a movement.

MATERIALS AND METHODS

Characterization of Biomechanics

There is a variety of biomechanical factors associated with any given movement, including passive inertia, interaction torques, muscle viscoelastic 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 end-point mobility and admittance (Hogan 1985a, 1985b, 1985c). End-point 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 viscoelastic properties of the arm. As normal dynamics are never altered, we 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 covary. Mobility on the plane may be mathematically expressed as a 2×2 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 2×2 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 biomechanics. The details of the calculation of the ellipse of mobility are described by Eq. 1, by transforming the inverse of the tensor of inertia from the joint into end-point space:

$$\mathbf{W}(\theta) = \mathbf{J}(\theta)\mathbf{I}^{-1}(\theta)\mathbf{J}'(\theta) \quad (1)$$

The mobility tensor $[\mathbf{W}(\theta)]$ is the inverse of the inertia tensor $[\mathbf{I}(\theta)]$. Equation 1 transforms the mobility tensor from joint space into end-point space using the Jacobian $[\mathbf{J}(\theta)]$ of the arm. As measures of arm inertia are not directly available, we used a planar two-segment rigid body model of the arm, characterizing each segment as a center of mass (m_s and m_e) located at a fraction (c_s and c_e) along the respective segment length (l_s and l_e), where subscripts s and e indicate the shoulder and elbow, respectively. Equation 2 shows the resulting formulation of $\mathbf{I}(\theta)$:

$$\mathbf{I}(\theta) = \begin{bmatrix} m_s c_s l_s + m_e l_s + m_e c_e l_e + 2m_e c_e l_s l_e \cos(\theta_e) & m_e c_e l_s l_e \cos(\theta_e) + m_e c_e l_e \\ m_e c_e l_s l_e \cos(\theta_e) + c_e l_e & m_e c_e l_e \end{bmatrix} \quad (2)$$

In Eq. 2, θ_e is the elbow angle, as defined in Fig. 1B. The remaining parameters are averaged mass and mass center distances, which have the following values: $m_s = 1.76$ kg, $m_e = 1.65$ kg, $c_s = 0.475$, and $c_e = 0.42$ (Sabes and Jordan 1997; Sabes et al. 1998). It is important to note that, in addition to mobility and admittance, there are a number of factors that capture elements of the muscular-skeletal system and may thus be considered as elements of biomechanics, e.g., muscle energy. However, in the present study, we preferred to use metrics that capture the biophysical properties of the arm, such as mobility or admittance, over energy, which could be viewed as a consequence of the former. Nevertheless, we performed control analyses to assess the influence of energy on target choices, which are described in the following sections.

Subjects

Twelve right-handed subjects (7 women and 5 men, average age: 29 yr) participated in this study (1 of whom also took part in our previous study). They had no known neurological disorders and normal or corrected to normal vision, and all were naive about the purpose of these experiments. Handedness was determined by a simplified version of the Edinburgh Handedness Inventory (Oldfield 1971). All subjects signed a consent form before initiating the experimental session. The experimental protocol was approved by the Institutional Review Board of the University of Montreal.

Task Apparatus

The task apparatus consisted of a digitizing tablet (GTCO Calcomp, Columbia, MD, 0.915×0.608 m) and a half-silvered mirror suspended 16 cm above and parallel to the digitizer plane. Visual stimuli were projected onto the mirror by an LCD monitor suspended 16 cm above the mirror, producing the illusion that the targets lie on the plane of the digitizing tablet (Fig. 1A). Subjects made movements using a digitizing stylus, held vertically in the hand, whose position was sampled at 125 Hz with a spatial resolution of $0.013 \text{ cm} \pm 0.127 \text{ mm}$. The surface of the digitizing tablet was coated with Vaseline to reduce friction.

Electromyographic (EMG) activity was recorded to assess differences in trajectory initiation and execution from three flexors (the pectoralis major, biceps long head, and brachioradialis) and three extensors (the triceps lateral head, triceps long head, and posterior deltoid). EMGs were measured with disposable MT-130 surface electrodes (King Medical, King City, ON, Canada), amplified ($\times 10,000$), and band-passed filtered (10–400 Hz) by an eight-channel Lynx-8 (Neuralynx, Bozeman, MT) and sampled at 1,000 Hz by an acquisition card (National Instruments, Austin, TX) installed on a personal computer running Windows XP (Microsoft, Redmond, WA). Maximum voluntary contraction (MVC) was estimated at the beginning of each task for each individual subject. The control of the behavioral task, stimulus display, and synchronization of task events and signal recordings were performed by a custom-written LabView program (National Instruments). Data from each

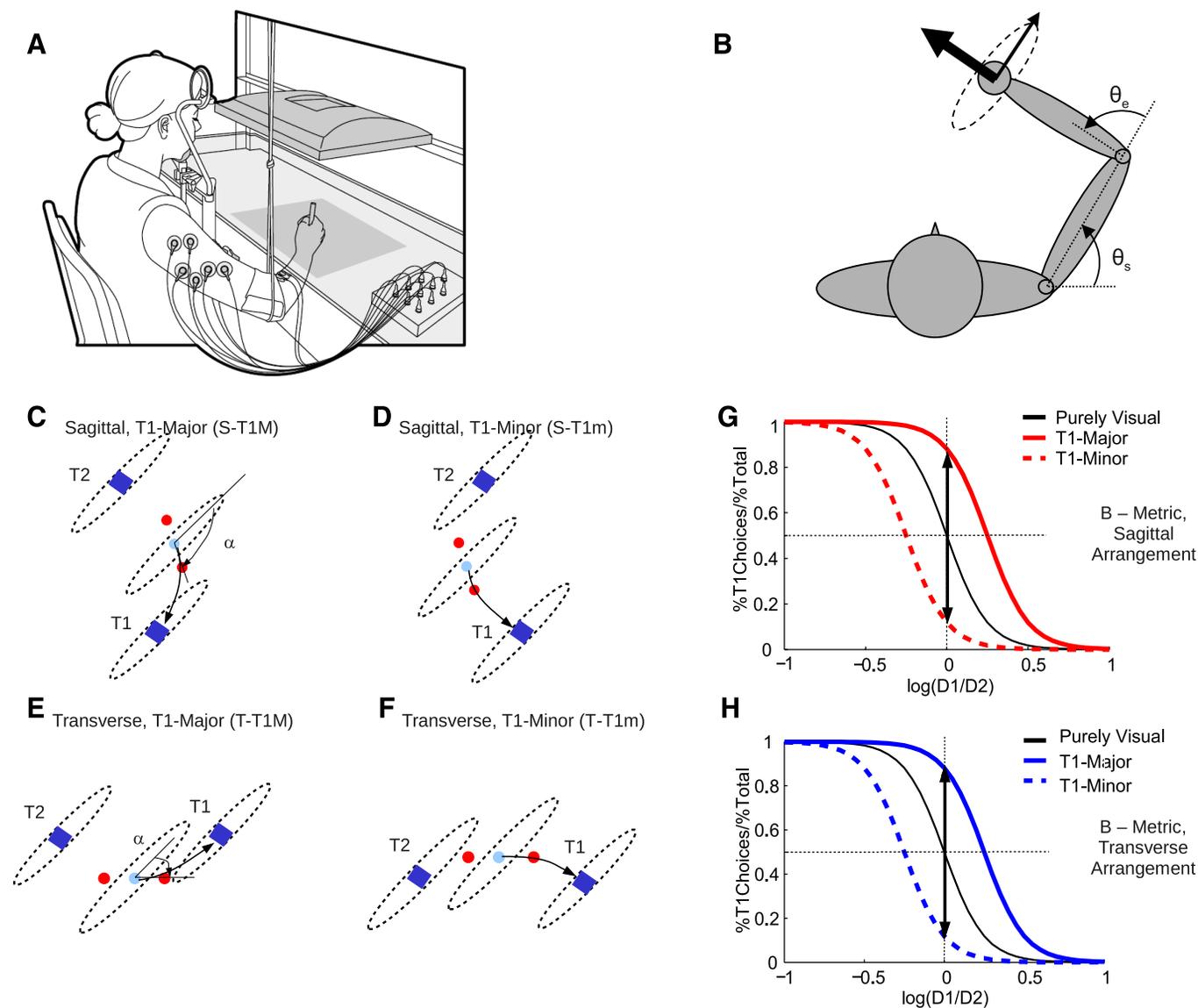


Fig. 1. Experimental paradigm. **A**: a subject was seated at the apparatus with her head in a chin rest and elbow in a sling that suspended the forearm approximately parallel to the digitizer surface. **B**: definition of the joint angles [θ ; at the elbow (θ_e) and at the shoulder (θ_s)] and mobility/admittance ellipse at the hand (dashed line). The thick arrow shows the large force required to accelerate the hand away and to the left, whereas the thin arrow shows the 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 (VPs; red dots) with respect to the starting circle (cyan dot). The dashed lines show the mobility ellipses at the origin and end of movements. The arrows show example trajectories to *target 1* (T_1). Note that in the T_1 major (T_1 -M) arrangements, the trajectory arrives at T_1 along the major axis of the mobility ellipse, whereas for the T_1 -minor (T_1 -m) arrangements, it arrives along the minor axis. T_2 , *target 2*; S, sagittal; T, transverse. **G**: predicted choice patterns for the sagittal stimulus arrangements (C and D). The x-axis is the log of the ratio of path distances (D) to T_1 versus T_2 , and the y-axis is the percentage of choices made to T_1 . If subjects preferred to arrive along the major axis of the mobility ellipse, then the choice function for the T_1 -M arrangement (solid line) should be shifted to the right of the choice function for T_1 -m arrangement (dashed line). If subjects do not take biomechanics into account, then the choice functions should be identical (black line). **H**: predictions for the transverse arrangements (E and F) using same format as in G. Metric B is the vertical distance between T_1 -M and T_1 -m preference curves for the case of equal relative distance.

session were transferred to a MySQL database (Oracle, Redwood City, CA) for further analysis using custom-designed Matlab scripts (Mathworks, Natick, MA).

Behavioral Task

The task involved making free choices between two potential reaching movements, each defined with a via point and target. Via points and targets were placed such that each movement was curved, with the final part of the trajectory aligned with either the major or minor axis of the arm's mobility ellipse (see Fig. 1, C–F). The total

path length was varied such that the two trajectories were either the same length (11 cm) or different lengths (10 vs. 12 cm or 9 vs. 13 cm). These two factors are explained in *Manipulation of Visual Versus Biomechanical Factors*. In separate blocks, two other factors were also manipulated, both concerned with the control of the end point. The first factor was the aiming accuracy, which was parameterized as a function of the width of the target (1 or 3 cm). The second factor was the constraint of stopping, which was implemented by instructing the subject to stop at the target or to punch through it and to stop whenever afterward. Each combination of these two constraints was performed in separate blocks, as

described in *Manipulation of Task Control Factors: Aiming and Stopping Requirements*.

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 trials) and one target (20 trials). 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: 1 cm), a via point (red dot, radius: 1 cm), and a target (dark blue square, sides: from 1 to 3 cm, depth: 1 cm; Fig. 1, C–F). Each trial began when the origin cue was shown on the screen and the subject placed the stylus into it. After a 300- to 700-ms center hold time, the stimuli defining one or two potential trajectories were shown. After an additional 500- to 700-ms observation time, a go signal was given (the origin cue disappeared). Subjects were instructed to react as fast as possible, to choose the action that felt the most comfortable, and to move the stylus over the via point and toward the target.

In the experimental cases in which the subject was supposed to stop at the target [aiming + stopping (AS) or stopping-only (S) conditions] and the subject did not manage to hold position at the target cue for 500 ms (target hold time), a target-hold error was logged. However, the error was not reported to the subject to avoid introducing error-dependent biases. Other criteria for a trial to be considered faulty were as follows: if the stylus left the origin before the go signal, if the reaction time was shorter than 200 ms or longer than 1,000 ms, or if the stylus reached the target before first crossing over the via point. Each individual trial was shown to the subject a single time. In other words, even if a trial were faulty, the sequence of trials continued to present the subject with the next trial. Error trials in which the subject crossed the via point but failed to enter the target or failed to stop at the target during the target hold time were considered for further analysis. Those error trials where the movement preceded the go signal were discarded. Visual feedback was provided during the movement by showing the stylus position as a small cross in real time. 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).

Manipulation of Visual Versus Biomechanical Factors

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, as described in Cos et al. (2011). To this end, we performed a comparative analysis of target preference between two cases in which we exchanged the biomechanical factors at each target (see Fig. 1, G and H, for the predicted effects). In other words, we arranged the via points and targets such that the path of the trajectory approaching a target was approximately aligned with either the major or minor axis of the arm's mobility/admittance ellipse, calculated at the target (cf. Fig. 1, C–F). Arrangements could assume one of two orientations: sagittal or transverse (see Fig. 1, C and D vs. E and F), depending on whether the movement options were, on the horizontal plane, either away or toward the subject's body or toward the right or left of the origin. Furthermore, arrangements could assume one of two biomechanical configurations: *target 1* (T_1) major or T_1 minor, depending on whether the path approaching T_1 was approximately aligned with either the major or minor axis of the arm's mobility/admittance ellipses, calculated at the target (cf. Fig. 1, C–F). For the sagittal arrangements (Fig. 1, C and D), the lower target was denoted as T_1 , and for the transverse arrangements (Fig. 1, E and F) the rightmost target was denoted T_1 . Thus, in the arrangements shown in Fig. 1, C and E, which we call the T_1 major condition, reaching movements to T_1 would arrive on a path aligned with the major axis of the mobility ellipse, whereas movements to *target 2* (T_2) would arrive on a path aligned with the minor axis. In contrast, in the T_1 minor" arrangements shown in Fig. 1, D and F, movements to T_1 would arrive along

the minor axis and movements to T_2 would arrive along the major axis.

In summary, trials were first classified as one-target or two-target trials, depending on whether the arrangement contained one or two targets, respectively. The one-target trials were included within each block for three main reasons: to mitigate habits (see *Mitigating the Effect of Habits*), to enforce practice of reaching movements towards all targets independently of the subject's preferences, and to provide sufficient data to study movement accuracy at the target at each geometric arrangement. However, the main body of trials consisted of the two-target trials, which allowed us to study the subject's target preference as a function of biomechanical and control constraint factors. To this end, subjects were required to make a free choice on each two-target trial and to perform a reaching movement toward one of the targets (blue squares, cf. Fig. 1, C–F), crossing over the via point associated with that target (red dots). The via points were placed in such a manner that launching biomechanics for both potential trajectories were equalized. Furthermore, to account for the possible confound of purely kinematic differences (hand path) at each trial, we alternated at random among the four possible geometric arrangements, classified according to their orientation as sagittal or transverse and to their arrival biomechanics, aligned to the major/minor axis of the ellipse at T_1 (T_1 major/ T_1 minor). Thus, to assess the influence of biomechanical and path distance factors on decision making, we compared the subjects' T_1 preferences for groups of trials between T_1 major and T_1 minor arrangements (see Fig. 1, G and H). To this end, we manipulated the "visual appeal" of each target by varying the relative path length from the origin through the via point and to each target. The total path lengths to T_1 versus T_2 were, respectively, 9 vs. 13 cm (20% of trials), 10 vs. 12 cm (20%), 11 vs. 11 cm (20%), 12 vs. 10 cm (20%), or 13 vs. 9 cm (20%). In general, subjects should be influenced both by the relative path distance between targets as well as by the relative energy involved in reaching toward either of them (Guigon et al. 2007).

It is important to note that from the perspective of the relative angular placement of the origin, the via points, and the targets, all four stimulus configurations were identical for each relative distance case. This means that factors dependent on relative path curvature should not influence choice preferences across the different configurations. Furthermore, T_1 was always in the lower half of the workspace during sagittal configurations and in the right half during transverse configurations, which means that any potential workspace preferences would always favor either T_1 or T_2 in each of the two orientations (sagittal or transverse) but would not vary between the T_1 major and T_1 minor conditions.

Manipulation of Task Control Factors: Aiming and Stopping Requirements

The specific goal of this study was to investigate how subjects make choices between reaching movements with different biomechanical properties as a function of the control constraints. In particular, we were interested in understanding how the control of the end point along the direction of movement and in the direction perpendicular to movement could potentially modulate the subjects' choices. Throughout this report, we will refer to the control along these two directions as stopping and aiming easiness, respectively. Stopping easiness refers to the control of the end point along the direction of movement and aiming easiness in the direction perpendicular to it. To test their effect, we adapted the experimental setup described by Cos et al. (2011) to accommodate the requirement of stopping and/or aiming at the target by defining four types of trials: unconstrained (U), S, aiming only (A), and AS, as shown in Fig. 2, A–D. Figure 2A shows the baseline condition (U), in which the subject was not required to stop at the target and the width of the target was three times larger than its depth. Figure 2B shows the S condition, in which the target was wide, relaxing the requirement of aiming accuracy, but the

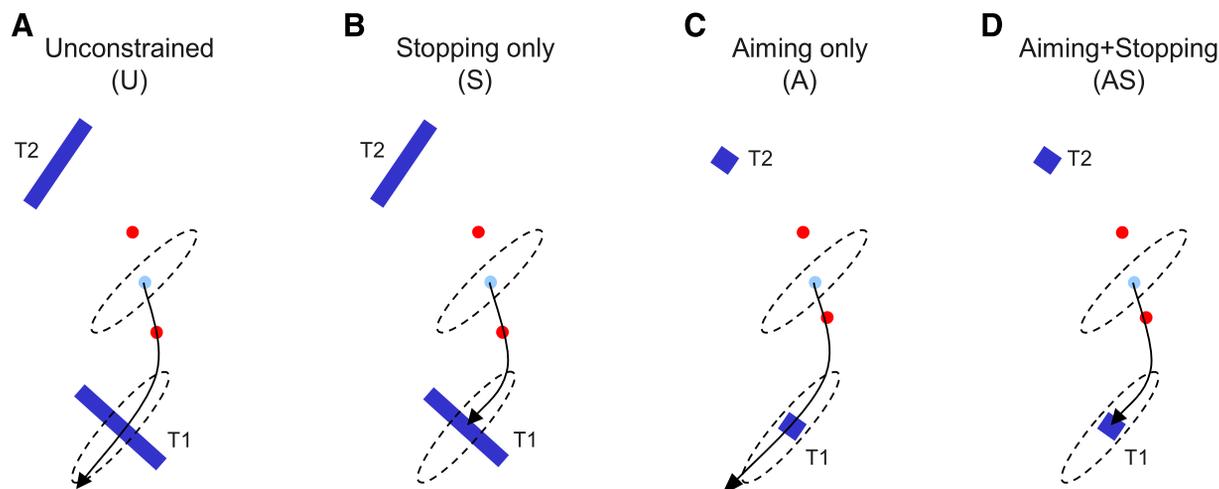


Fig. 2. List of experimental control conditions shown in the sagittal T_1 -M arrangement and in the equal target relative distance case. All four conditions [unconstrained (U), stopping only (S), aiming only (A), and aiming + stopping (AS)] parameterize biomechanics in the same manner and could be presented throughout the task in one of the four geometric arrangements shown in Fig. 1. However, the requirements of end-point control near the target varied substantially across conditions. *A*: targets in the U (or baseline) condition were wide and easy to aim at and had to be crossed over before stopping. *B*: targets in the S condition were also wide and easy to aim for; however, the subject was required to stop at the target. *C*: targets in the A condition were small and had to be crossed over before stopping. *D*: targets in the AS condition were small, and the subject was required to stop in them.

subject was instructed to stop within it. Figure 2C shows the 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, Fig. 2D shows the 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.

Mitigating the Effect of Habits

Because we were interested in investigating how biomechanics and the control of the end point at the target influence motor decisions, we wanted to reduce the influence of potentially confounding factors such as past experience and error rates associated with each target. First, we made target positions unpredictable from trial to trial by presenting them at random, either in an approximately sagittal orientation (Fig. 1, C and D) or an approximately transverse orientation (Fig. 1, E and F), each with either the T_1 major or T_1 minor configuration. This made it equally probable on any given trial that the “easier” movement would begin in one of the four cardinal directions (subjects performed a minimum of 15 trials of each type). Second, we interspersed two-target trials with single-target trials corresponding to each arrangement (path length of 11 cm only). This forced subjects to acquire substantial experience with making movements to each of the different targets along each possible trajectory. This was done so that error rates across configurations were generally balanced and so that we could analyze the kinematics and dynamics of movements that would otherwise be avoided if subjects were given a choice.

Analyses

The analyses described here aim describe the procedure to quantify the modulatory effect exerted by the stopping and aiming control constraints on the subject’s target preference. First, we calculated T_1 preference curves for each of the four types of control constraints (U, S, A, and AS) by calculating the number of times that subjects selected T_1 divided by the total number of choices at each of the geometric arrangements (sagittal T_1 major, sagittal T_1 minor, transverse T_1 major, and transverse T_1 minor) for each of the five relative distances between targets. Second, in each of the four arrangements, the T_1 preference [$P_{T_1}(Q)$] values were plotted on a logarithmic scale and fitted with a sigmoidal curve, as described by Eq. 3:

$$P_{T_1}(Q) = \frac{\exp(Q)}{1 + \exp(Q)}, \text{ where } Q = a \times \left[\log\left(\frac{D_1}{D_2}\right) \right] + b \quad (3)$$

where a and b are the parameters fitted for data from each configuration and D_1 and D_2 are the relative distances to T_1 and T_2 , respectively, measured along the path from the origin through the via point and to the target. The design of the geometric arrangements, for the sagittal and transverse orientations, was aimed at maximizing the difference of biomechanical factors between targets. This difference has been shown to play a major role in the selection of the target (Cos et al. 2011).

Once the T_1 preference curves were computed for each control constraint condition (U, S, A, and AS), we assessed the modulatory effect of the end-point control constraints, namely, aiming and stopping at the target. To do this in the most systematic manner, and to individually quantify the effect of each specific control constraints, we organized the comparisons in three groups, depending on whether the analysis focused on the effect of the stopping requirement (AS vs. S and A vs. U cases), on the effect of the aiming requirement (AS vs. A and S vs. U cases), or a combination of both (AS vs. U and A vs. S cases). To determine the differences between the preference curves, we performed a bootstrap test (Efron 1982). In brief, we first measured the differences in size of the vertical shift between preference curves obtained for T_1 major versus T_1 minor configurations at equal distances across the different control constraints. We call this metric B (see Fig. 1, G and H). We then compared the difference of B values between control constraint conditions with the distribution of difference B values obtained from 10,000 shuffled data sets of the preference values of the two conditions being compared. If the experimental value of the metric B difference was $>95\%$ of the values obtained from shuffled data, the result was considered significant at $P < 0.05$.

In addition to this, differences of end-point scatter across different control constraints were assessed with paired Kolmogorov-Smirnov (KS) tests. Our threshold of significant difference was $P < 0.05$.

Muscle Work

In addition to kinematic factors, it seems logical to assume that effort or energy may exert some influence on decision making. To calculate the dependence of decisions on energy, we estimated the preference for T_1 over the total number of decisions as a function of

the relative muscle work implicated in moving the arm from the origin to one of the two targets for all five possible relative D_1/D_2 . The muscle work involved in each movement was approximated as the muscle work necessary to move the arm from origin to target, through the via point, as described by Eq. 4, discounting the contribution of interaction torques (cf. Eq. 4):

$$W = \int_{\text{Origin}}^{\text{Target}} \tau_m d\theta \quad (4)$$

where W is the muscle work, and τ_m is the torque necessary to move the arm from the origin to the target position, expressed in angular coordinates.

As for the sigmoids expressed as a function of relative target distance, the proportion of T_1 choices for each arrangement (sagittal T_1 major, sagittal T_1 minor, transverse T_1 major, and transverse T_1 minor) was plotted on a logarithmic scale and fitted with a sigmoidal curve as described by Eq. 5 [where W_1 is work (energy) involved in action 1 and W_2 is work involved in action 2]. We performed the following calculation separately for each of the four types of trials (U, S, A, and AS) for the T_1 major versus T_1 minor arrangements:

$$P_{T_1}(R) = \frac{\exp(R)}{1 + \exp(R)}, \text{ where } R = a \times \left[\log\left(\frac{W_1}{W_2}\right) \right] + b \quad (5)$$

To determine the significance of the effect of biomechanics between preference curves obtained for T_1 major versus T_1 minor arrangements, we used the bootstrap technique (Efron 1982). In brief, we first measured the size of the shift by calculating the distance between preference curves obtained for T_1 major versus T_1 minor configurations at equal distances. We called this metric D , as in our previous study (Cos et al. 2011). We then compared this value of D to the distribution of D values obtained from 10,000 shuffled data sets, in which the preference values obtained for the five relative distances were randomly shuffled between major versus minor configurations. If the value of D was $>95\%$ of the distance values obtained from shuffled data, the result was considered significant at $P < 0.05$.

Furthermore, to determine the contribution of launching cost, we performed a comparative analysis between the muscle work necessary to move the arm from the origin to each of the two via points within each arrangement. The calculation of the muscle work was analogous to the one described above (see Eq. 8) but integrated between the origin and the via point only.

Muscle Activity, Muscle Wasted Contraction, and Useful Contraction

In addition to analyzing the sequence of muscle activations for each potential movement across control constraint conditions, we also performed an analysis of how muscle energy is expended during movement execution across conditions. Specifically, we first used EMG signals from three upper arm muscle pairs [two shoulder monoarticulars (the pectoralis major vs. posterior deltoid), two shoulder-elbow biarticulars (the biceps long head vs. triceps long head), and two elbow monoarticulars (the brachioradialis vs. triceps lateral head)] to calculate the wasted contraction (WC; or cocontraction) and useful contraction (UC) for each movement. We used these to perform a comparative analysis of the differences of energy cost across the different control constraint conditions (U, S, A, and AS). EMG signals were normalized using the MVC recorded for each individual muscle and subject at the beginning of each session.

The cocontraction (or WC) was calculated as the sum, across the three pairs of antagonistic muscles, of the minimum contraction of each pair (Thorughman and Shadmehr 1999), as described by Eq. 6:

$$WC = \sum \text{minimum}(u_{\text{agonist}}, u_{\text{antagonist}}) \quad (6)$$

In a similar fashion, we also calculated the level of UC for each movement using the same normalized EMG signals, as the net contraction of the agonist muscle (u_{agonist}) minus the antagonist muscle ($u_{\text{antagonist}}$) for each muscle pair during movement execution, as described by Eq. 7:

$$UC = \sum (u_{\text{agonist}} - u_{\text{antagonist}}) \quad (7)$$

Normalization of Contraction

The nature of this experiment, in which we measured the influence of the requirement of stopping at the target and aiming at the target on decision making, inevitably yielded movements with different kinematics for the different constraint conditions. Most importantly, peak velocity and movement duration can be quite different whether stopping is required or not. Thus, any potential analysis of the raw muscle contraction to quantify the effect of the task requirements (aiming/stopping) would inevitably be confounded by differences in velocity across the conditions. Hence, to make it possible to quantify the cost of performing a controlled arrest or of carefully aiming at a target via comparative analysis of contraction across control constraint conditions, it is necessary to perform normalization such that both execution time and peak velocity across conditions are at least approximately comparable. However, although most straightforward, a normalization by peak velocity or execution time separately would not be appropriate, as the resulting cocontraction values would not be consistent with any real kinematic values because the differences are not only a matter of peak value but are also encompassed by an expansion or reduction of execution time. Thus, instead of more classical normalization methods, we applied two different procedures to normalize muscle contraction. The first procedure consisted of normalizing contraction by the integral of the tangential velocity and the second procedure consisted of normalizing contraction by the integral of the transport energy (see Eq. 8), with both integrated from movement onset until peak velocity. Furthermore, although the normalization was performed for both metrics of contraction throughout the entire movement, the calculation of the normalization constants was obtained by considering the initial phase of the movement only, as we were interested in the differences of end-point controllability during target arrival only. Both of these normalization methods equalize differences in peak velocity and the expansion of movement duration simultaneously and, therefore, serve the purpose of quantifying the contraction applied to control the end point along and perpendicular to the direction of movement across control constraint conditions. However, these are merely rough estimates, and that any resulting value will only yield an approximation of how energy is expended throughout movement as a function of the control constraints.

Once the normalization was performed, we analyzed the contributions of WC to the stabilization of the end point along the direction of movement [stopping cocontraction (WC_S)] and perpendicular to it [aiming cocontraction (WC_A)] by comparing the normalized WC across conditions. As expressed by Eq. 8:

$$WC = WC_S + WC_A \quad (8)$$

the WC in the AS condition may be decomposed into two components: a component derived from the requirement of stopping at the target (WC_S) and another component derived from the requirement of aiming carefully at the target (WC_A). Specifically, to calculate the WC_S component, we subtracted the WC of the S case from the WC in the U case. Similarly, to calculate the WC_A component, we subtracted the WC of the A case from the WC in the U case. We followed the same operation to calculate the aiming and stopping components of UC (UC_S and UC_A). Furthermore, although we first presented the amount of control as a percentage of control contraction, we consid-

ered that it is useful to relate contraction to energy, as this may help to complete the picture of how energy is expended for each control constraint condition. Thus, as shown by Eq. 9:

$$C = WC + UC \quad (9)$$

muscle contraction (C) may be decomposed into two components: WC and UC . To relate contraction to metabolic energy, we assumed UC to be proportional to transport energy, calculated as the integral of the torques, obtained from the equations of inverse dynamics throughout the movement (see Eq. 4). We then used the same constant relating UC and transport energy to calculate a rough estimate of the energy corresponding to each component of wasted contraction (WC_S and WC_A).

Movement Onsets and Offset

We detected the time of movement onset by determining the moment at which either coordinate of the cursor position (x,y) first differed from its resting value within 200 ms of the go signal. Likewise, the time of movement offset was calculated as the moment at which the end-point position did not differ from its previous value for >50 ms after the stylus entered the target.

RESULTS

Choice Preferences

To assess the effect of the aiming and stopping constraints on the subjects' preferences, we calculated preference curves for T_1 (see MATERIALS AND METHODS) at each of the four geometric arrangements (sagittal T_1 major, sagittal T_1 minor, transverse T_1 major, and transverse T_1 minor; see Fig. 1, *C–F*) and under each of the four constraint conditions (U, S, A, and AS; see Fig. 2, *A–D*). The preference curves, calculated by collapsing the choices across all subjects for each target and relative distance, are shown for each condition in Fig. 3, *A–D*. As shown in Fig. 3, *A–D*, there was a significant influence of path distance on the target chosen, with T_1 selected more often when that target was the closer of the two. Furthermore, in agreement with our previous study (Cos et al. 2011), T_1 preference curves exhibited a significant shift between T_1 major and T_1 minor arrangements, thus demonstrating that the biomechanical difference between the movements exerts a significant influence on target choices. Typically, the curve for the T_1 major condition was shifted to the right of the curve for the T_1 minor condition ($P < 0.05$ by bootstrap test), indicating that in the T_1 major arrangement, T_1 is more appealing than T_2 , even when its distance from the origin is larger. This difference in target preference, as a function of the path trajectory alignment (i.e., the effect of biomechanics), was quantified with metric B (see MATERIALS AND METHODS and Fig. 3).

To control for the potential effect of learning on the subjects' target preferences, we performed an analysis of practice on some of the subjects, focusing on sets of 150 trials at intervals of 150 trials across each session. The results (which are not shown) were similar throughout the entire session, therefore suggesting that the target preference across each session stabilized rapidly after the first 100–150 trials and that little variability was observed from then onward. This confirms that the preference for major trajectories does not require extensive practice.

Furthermore, the first analysis of the four T_1 preference curves across control constraints (see Fig. 3) revealed that the

effect of biomechanics between T_1 major and T_1 minor arrangements diminished as more constraints were gradually imposed to control the end point. Figure 3 shows that metric B (see MATERIALS AND METHODS) was largest for the U condition. However, as we reduced the width of the target and enforced the requirement of aiming (the A case), the metric B value diminished only a little, indicating that aiming does not strongly modulate the effect of biomechanics. In contrast, in the S case, the metric B value was 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 metric B values between the S and AS cases, in which both aiming at a small target and stopping are required, were 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.

Analysis of Kinematics

Figure 4, *A–D*, shows typical trajectories obtained in the two-target trials for each of the four geometrical arrangements shown in Fig. 1, *C–F* (sagittal T_1 major, sagittal T_1 minor, transverse T_1 major, and transverse T_1 minor) for targets at equal relative distances (11 cm). A visual inspection of the number of trajectories directed toward each target in the least (U) and most (AS) constrained cases highlighted that although there was a bias of the subjects' choices toward major targets, this bias was the strongest in the absence of constraints. This replicates the results of our first study (Cos et al. 2011) by showing that, all other factors being equal, subjects exhibited a tendency to reach toward the target offering a major arrival. It also shows that the demands of the four control constraint conditions also exert a significant modulation of the subjects' choices. This suggests that a prediction of the end-point controllability at the target does influence the process of action selection, as a reaching movement has to be chosen before initiation. Specifically, a comparison of the relative number of trajectories toward each target between the U and A cases (see Fig. 4, *A* and *C*) showed that waiving the aiming requirement by making the targets wider resulted in a mild increase of the number of trajectories toward the major target. Furthermore, a comparison between the U and S cases (Fig. 4, *A* and *B*) showed that relaxing the stopping requirement provokes a dramatic increase of the number of trajectories toward the major targets in all four geometric arrangements. Consistently with this, a similar tendency was observed from a comparison between the baseline U and AS cases (Fig. 4, *A* and *D*), thus reinforcing the view that the requirement of controlling the end point to stop at the target exerts a strong modulation of the effect of biomechanics on the subjects' choices.

Figure 4, *E* and *F*, shows the tangential velocity profiles for reaching movements toward T_1 and T_2 for a typical subject for each arrangement and control constraint condition (see color coding), aligned at the time the stylus enters the via point. Overall, although the profiles exhibited significant variability among con-

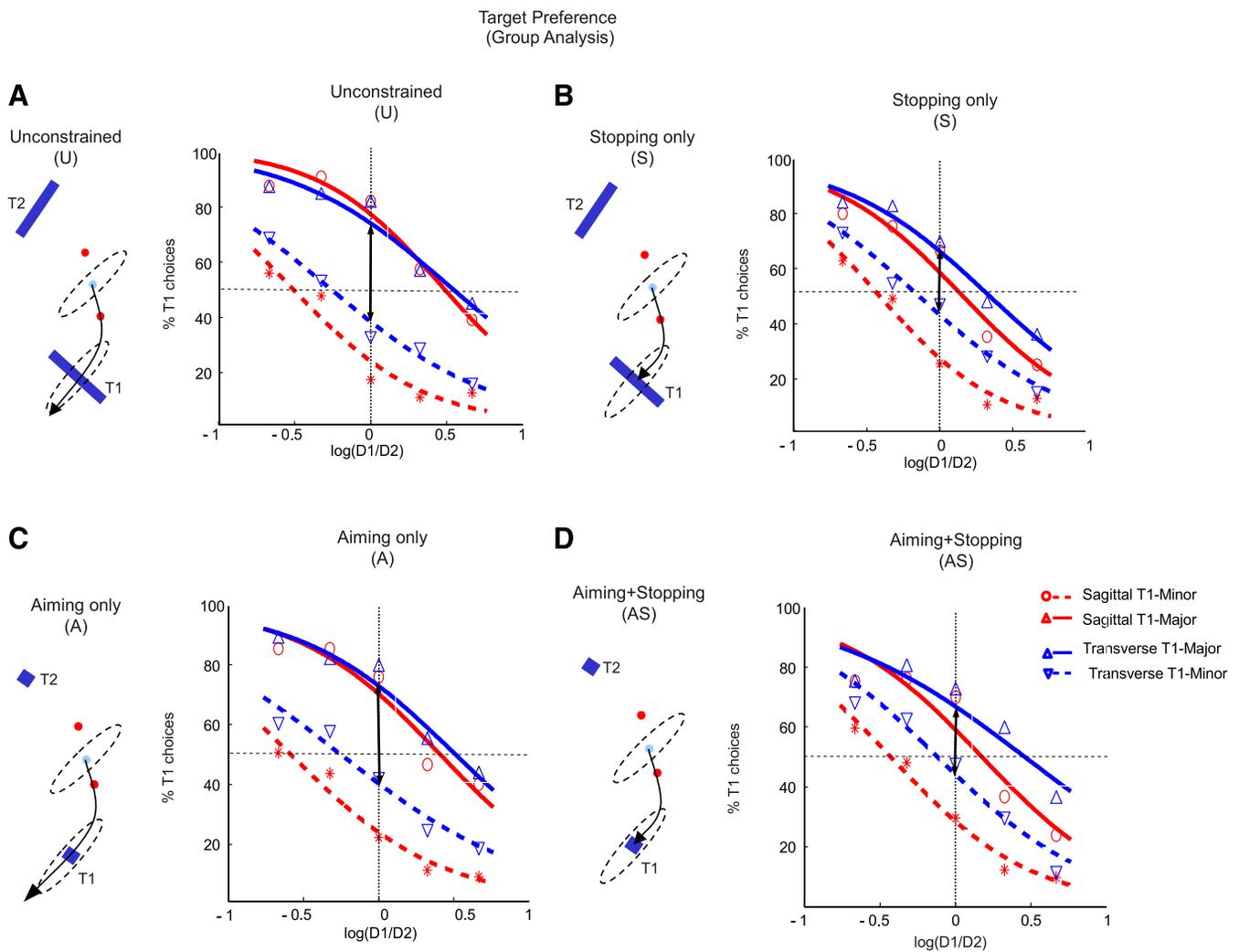


Fig. 3. Group analysis of T_1 preference curves for each control condition (U, S, A, and AS; see depictions at the top of the preference curves). A: U (or baseline) case. B: S case. C: A case. D: AS case. The raw data dots were fitted with sigmoidal curves for T_1 -M (solid curves) and T_1 -m (dashed curves) in the sagittal (red) and transverse (blue) arrangements. Note that in all cases, T_1 -M curves were to the right of T_1 -m curves, showing that T_1 was chosen more frequently in its major configuration under each experimental condition and geometric arrangement. Furthermore, the first observation indicated that the requirement of stopping at the target diminished the effect of biomechanics between targets; thus, the distance between solid and dashed sigmoids was shorter in those conditions in which stopping was enforced (S and AS) than under those in which the stopping requirement was relaxed (U and A) (metric B: $B_U > B_S > B_{AS}$).

straint conditions, they all tended to be smooth and single peaked. Furthermore, the profiles were not symmetric, with a shorter acceleration phase than deceleration phase (probably because of the requirement of crossing over the via point). This was consistent in each of the four geometric arrangements. Importantly, the peak velocity was significantly higher in the conditions in which stopping was not required (A and U conditions) than in the conditions in which stopping was mandatory (AS and S conditions). Interestingly, although peak velocity was, on average, 30% higher when stopping was not required, the duration of the movement across all four conditions was remarkably similar. In other words, the cursor reached the target slightly after peak velocity when stopping was not required, meaning that the different constraints in the direction of movement and perpendicular to it control the velocity with which the movement is performed, but not the time of execution.

Influence of the Stopping Constraint

In addition to calculating the preference functions in all four experimental conditions (see Fig. 3), we also analyzed the

influence of the control constraints in each condition both along the direction of movement (what we call the stopping effect) and in the direction perpendicular to it (the aiming effect, which is described below). We performed two complementary analyses: an analysis of the outcome of the decision-making process itself via a comparison of target preferences between stopping and nonstopping conditions and a comparative analysis of end-point scatter distributions (off-axis), as a measure of control during target arrival. As here we focus on the effect of the stopping requirement, Fig. 5 shows these two analyses comparing between stopping and nonstopping conditions (U vs. S and A vs. AS conditions) for both the sagittal and transverse arrangements.

A visual assessment of the T_1 preference curves of the S versus U comparison and the AS versus A comparison showed that the requirement of stopping at the target typically reduced the biomechanics effect on the subjects' preference for the major target and a magnification of their preference for the minor target (see Fig. 4, A–D). In other words, the preference for T_1 in its major configuration was typically larger in the cases in which stopping at the

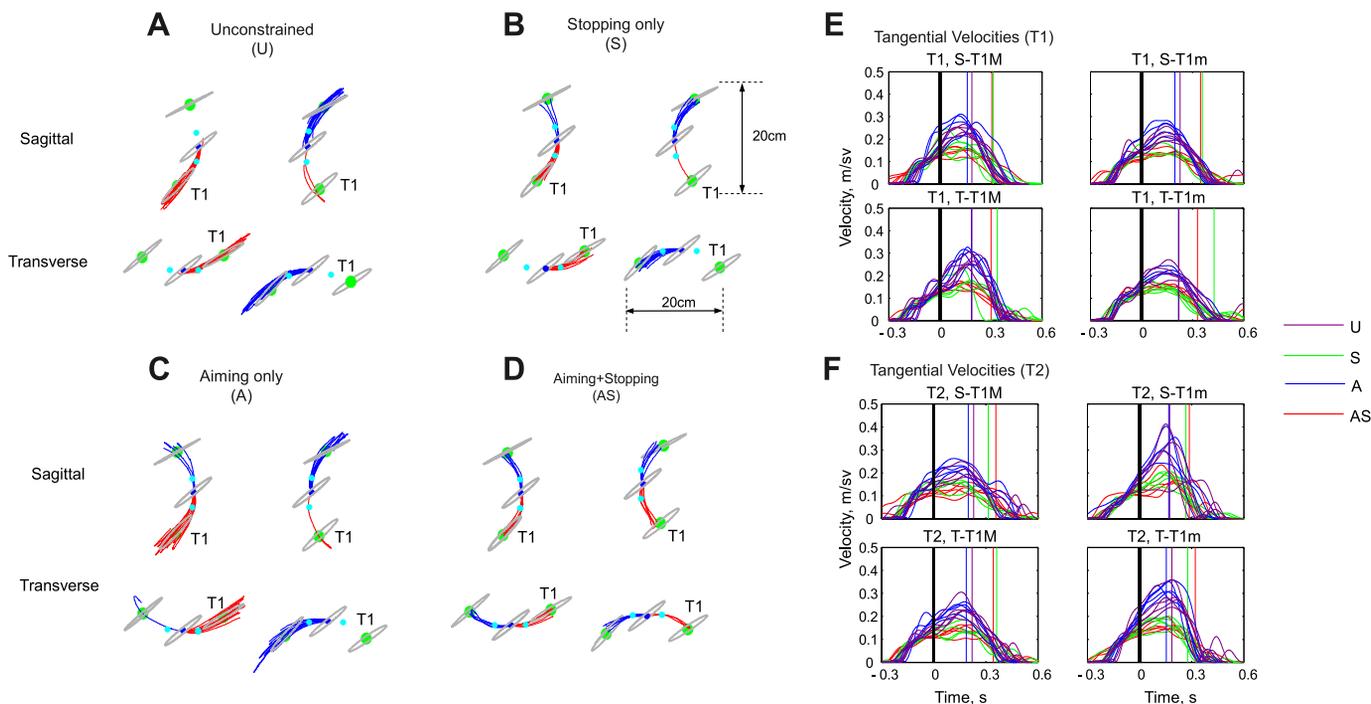


Fig. 4. Example kinematics. *A–D*: typical end-point trajectories for the case of equal relative distances to T_1 and T_2 for each experimental condition (U, S, A, and AS) in each geometric arrangement. For visualization purposes, trajectories toward T_1 are plotted in red and trajectories toward T_2 are plotted in blue. *E*: tangential velocities for trajectories aimed to T_1 for a typical subject in each geometric arrangement (sagittal T_1 -M, sagittal T_1 -m, transverse T_1 -M, and transverse T_1 -m) aligned on VP crossing. The curves are color coded according to experimental conditions, and vertical lines indicate target arrival. Notice that although the peak velocity across conditions varied significantly, the execution time remained relatively constant if we considered the entire movement. *F*: tangential velocities for trajectories aimed at T_2 for a typical subject (in the same format as in *E*).

target was not required than in those in which stopping had to be controlled. To quantify the influence of the stopping constraint on the subjects' aiming accuracy, we compared the subjects' preference curves and scatter distributions between S vs. U conditions (aiming was not required in either of them) and AS vs. A conditions (aiming was required in both of them). The results are shown in Fig. 5.

S versus U conditions. This first comparison (S vs. U) assessed the effect of stopping when aiming was waived in all cases. Differences in the transverse arrangement (Fig. 5*B*) were similar to those observed in our first visual assessment shown in Fig. 4, although they extended in this case over the entire range of relative target distances. This tendency was also maintained in the sagittal orientation (Fig. 5*A*), although target preference differences were much smaller. Furthermore, consistently with the differences in target preference, the off-axis scatter distribution exhibited a tendency to be wider when stopping was not enforced (see Fig. 7, *A* and *B*). However, differences were only significant ($P < 0.05$ by KS test) for the transverse T_1 major configuration. Therefore, the requirement of stopping when precise aiming was not enforced decreased the likelihood of targets in their major configuration to be selected and, in some cases, reduced the SD of the scatter distribution.

AS vs. A conditions. In a complementary fashion, the comparison of AS versus A cases assessed the control along the direction of movement when aiming was enforced (narrow targets). Enforcing stopping at the target decreased the likelihood of targets in their major configuration to be selected (Fig. 5, *C* and *D*) as well as the average end-point scatter (see Fig. 7, *C* and *D*). However, unlike for the previous case, the

requirement of careful aiming at the target across these experimental conditions enforced the differences both in preference curves and end-point scatter. Thus, whenever the requirement of stopping was enforced (AS case), the difference in major versus minor preference curves was reduced with respect to the case in which stopping was relaxed (A case), for both the sagittal and transverse orientations (see Fig. 5, *B* and *D*). However, this effect did not modulate the subjects' choices with the same intensity at each relative target distance; its effect was the largest ($P < 0.0001$) when D_1/D_2 was maximal for the transverse arrangement and D_1/D_2 was minimal for the sagittal arrangement (see Fig. 5*C*). Furthermore, consistent with the preference curves, the off-axis scatter obtained at the moment the end point entered the target (see Fig. 7, *A–D*) showed that only the scatter distributions for the T_1 major arrangements exhibited a significantly smaller variability when stopping was enforced than when it was relaxed, for both the sagittal and transverse arrangements ($P < 0.05$ by KS test). This was most likely the result of the larger peak velocities whenever stopping was relaxed. Remarkably, the differences of scatter distribution were only significant in the T_1 major arrangements.

As clearly shown in Fig. 5, the effect of stopping was larger for the transverse arrangement than for the sagittal arrangement. Although we cannot provide a conclusive answer, we believe that this may be explained by the nature of the movements compared. Sagittal arrangements require biarticular movements with a strong shoulder component, whereas transverse arrangements mostly require elbow movements. As a consequence, the launching energy to start sagittal movements is typically larger than to start transverse movements. Since the

Stopping Effect: T1 Preference Curves

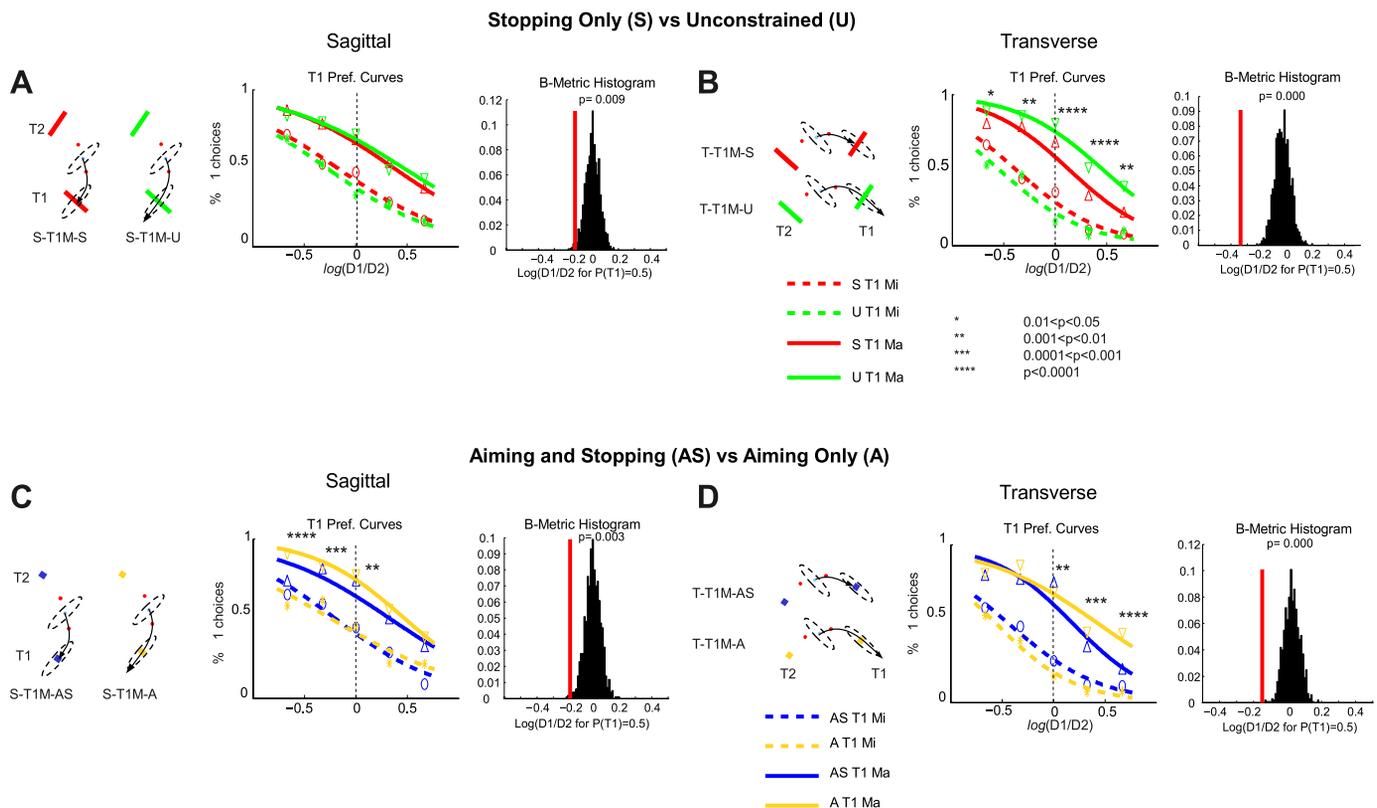


Fig. 5. Two cases of comparative analysis of the effect of stopping at the target across subjects. *A* and *C*: S vs. U cases, where aiming at the target was easy in both cases. *B* and *D*: AS vs. A cases, where aiming at the target was hard in both cases. *A* and *B*: T₁ preference curves for the S and U conditions for the sagittal and transverse arrangements. The asterisks at the top of the preference values indicate the statistical significance of the difference between cases for that value of target relative distance. The far right graph shows the *B* metric (red bar) between S and U conditions calculated at the point of equal distance compared against the distribution (black histogram) of bootstrapped *B* metric values. *C* and *D*: T₁ preference curves for the AS and A conditions for the sagittal and transverse arrangements. The far right graph shows the *B* metric (red bar) between AS and A conditions calculated at the point of equal distance compared against the distribution (black histogram) of bootstrapped *B* metric values.

target bias is due to the difference of biomechanical cost at each target, this difference is less salient in the sagittal case, which could explain why subjects were in general less sensitive to the difference of biomechanical cost between major and minor targets in the sagittal arrangements.

Overall, the first analysis suggested that the requirement of stopping reduces the effect of arm biomechanics on the decision-making process. Furthermore, although the aiming requirement refers to the control of the end point in the direction perpendicular to movement, the magnification of the effect when aiming is also required suggests interdependence between the control of the end point along the direction of movement and perpendicular to it. To further investigate this, we present a complementary analysis of the effect of aiming below.

Influence of the Aiming Constraint

Here, we characterized the effect of the aiming constraint using the same metrics as above: T₁ preference curves and end-point scatter. Figure 6 shows the differences of T₁ preference curves and scatter distributions between aiming and nonaiming conditions (A vs. U and AS vs. S) for sagittal and transverse arrangements.

The first visual assessment the results shown in Fig. 3 showed that aiming exerted a mild influence on the subjects'

target preferences. To quantify this, we compared cases varying the aiming condition, namely, the A and U conditions [both cases in which the stopping requirement was relaxed (Fig. 6, A and B)] and AS and S conditions [both cases in which stopping at the target was enforced (Fig. 6, C and D)].

A versus U conditions. We first assessed the effect of aiming by comparing the differences of subjects' T₁ preference between A and U cases. Although the differences were typically small, the bias for the major target was lower when aiming was required. This was largest when D_1/D_2 was minimal. Furthermore, the off-axis end-point scatter distribution tended to be smaller when aiming was enforced, but this was significant ($P < 0.05$ by KS test) only for the transverse arrangement (see Fig. 7, E and F).

AS versus S conditions. The second comparison assessed the effect of aiming between the AS and S conditions (stopping at the target was enforced in both of these conditions). In this case, aiming did not appear to exert any visible effect on the subjects' target preference, for both the sagittal and transverse arrangements (see Fig. 6, C and D). In contrast, the distributions of off-axis scatter did exhibit significant differences (see Fig. 7, G and H), with the average scatter being larger when aiming was relaxed for both the sagittal and transverse arrangements, although this difference was only significant for the

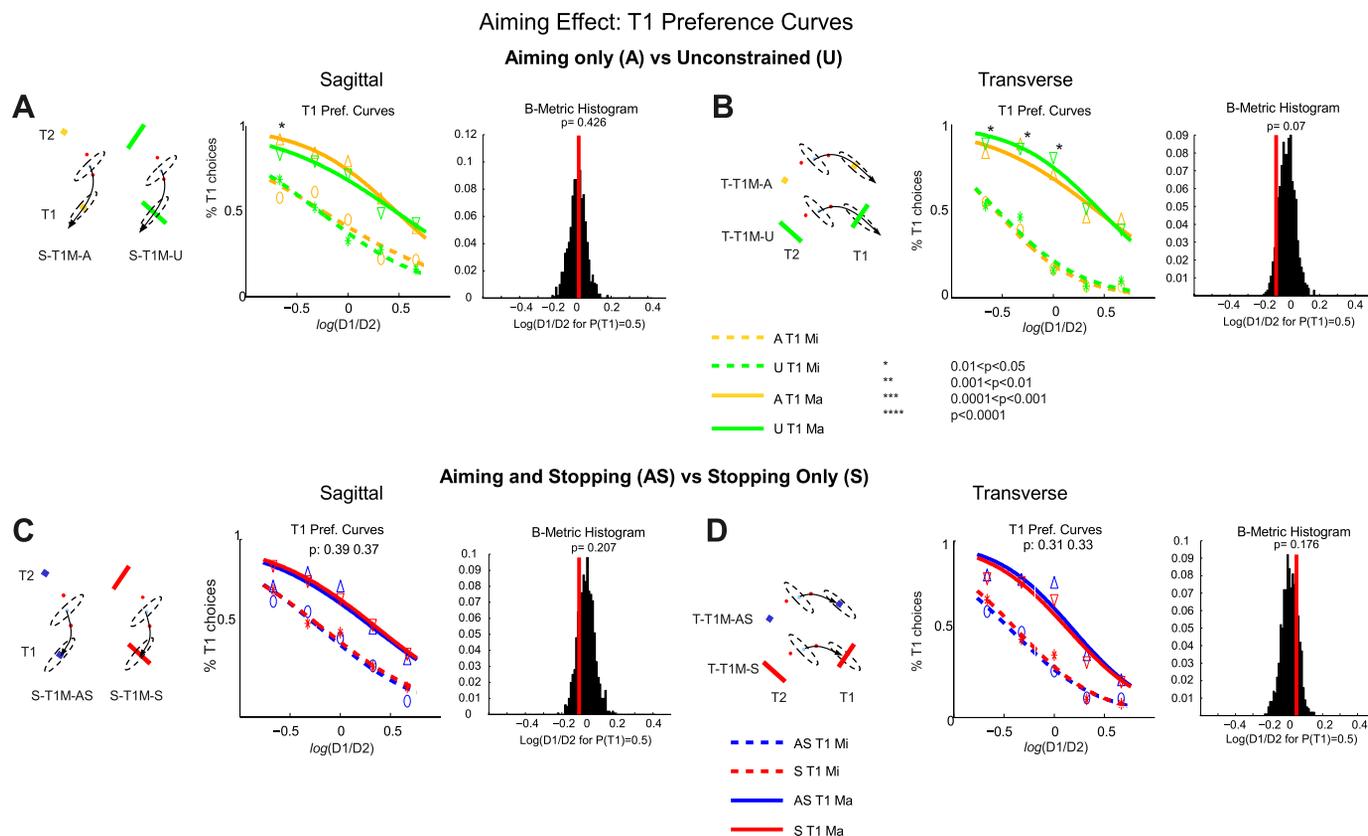


Fig. 6. Two cases of comparative analysis for the effect of aiming across subjects. *A* and *C*: A vs. U cases, where stopping at the target was not required in both cases. *B* and *D*: AS vs. S cases, where stopping at the target was required in both cases. *A* and *B*: T₁ preference curves for the A and U conditions for the sagittal and transverse arrangements. The number of asterisks at the top of each preference value indicates the degree of significance at that target relative distance. The far right graph shows the B metric (red bar) between A and U conditions calculated at the point of equal distance compared against the distribution (black histogram) of bootstrapped B metric values. *C* and *D*: T₁ preference curves for the AS and S conditions for the sagittal and transverse arrangements. The far right graph shows the B metric (red bar) between AS and S conditions calculated at the point of equal distance compared against the distribution (black histogram) of bootstrapped B metric values.

major target ($P < 0.05$ by KS test). We argue that this difference in scatter may be due to the difference of target width, as the narrow target increased the need of control in the direction perpendicular to movement without significantly altering target preference.

As shown in Fig. 6, the effect of the aiming constraint on the target preference was mild, at least compared with the effect of the stopping constraint. Nevertheless, the end-point variability in A and AS conditions was significantly larger than in U and S conditions, respectively (see Fig. 7, *E* and *H*). This indicates that although the requirement of aiming to a narrower target demanded a stricter control strategy in the direction perpendicular to movement, the cost of this strategy was not very influential on the process of decision making.

Analysis of Energy

Throughout this report, we assumed that the main biomechanical differences between the two movement options occur during arrival to the target and that costs during the launching phase were equalized. This is straightforward for the factors of mobility/admittance, because the via points were placed in opposite directions from the origin. However, to ensure that energy was also approximately equalized, we calculated the net muscle work (see Eq. 4) for each average movement within each arrangement and control constraint condition and compared the results obtained

between reaching movements. The calculation of energy was performed during two phases: movement initiation (from onset to the via point) and target arrival (from the via point to the target). Figure 8A shows both of these results, demonstrating that the energetic differences between movements during the launching phase were minimal, whereas the differences during the arrival phase were very significant. KS tests between major and minor configurations during the launching and arrival phases showed that the differences were significant ($P < 0.05$) in a regular fashion during the target arrival phase only. Thus, differences in target preference must rely on factors other than launching energy. In other words, the decision cannot be simply determined by the ease of initiating either reaching movement (like sliding along a valley of an energy surface) but must take other factors, such as predicted biomechanics, into account. This issue was examined in our previous study using a control experiment with a single via point (Cos et al. 2011, Supplement Material), and we will return to it in the DISCUSSION.

We also assessed the influence of the relative movement energy on the subjects' choices by calculating the subject's T₁ preference as a function of the average relative net muscle work of each movement (see MATERIALS AND METHODS), as shown in Fig. 8B. Although the values of relative energy within each arrangement varied with relative target distance, their range of variation was remarkably narrow, thus yielding close to vertical preference curves. In contrast, differences of relative energy between major

Stopping Effect: Off-Axis Scatter Histograms

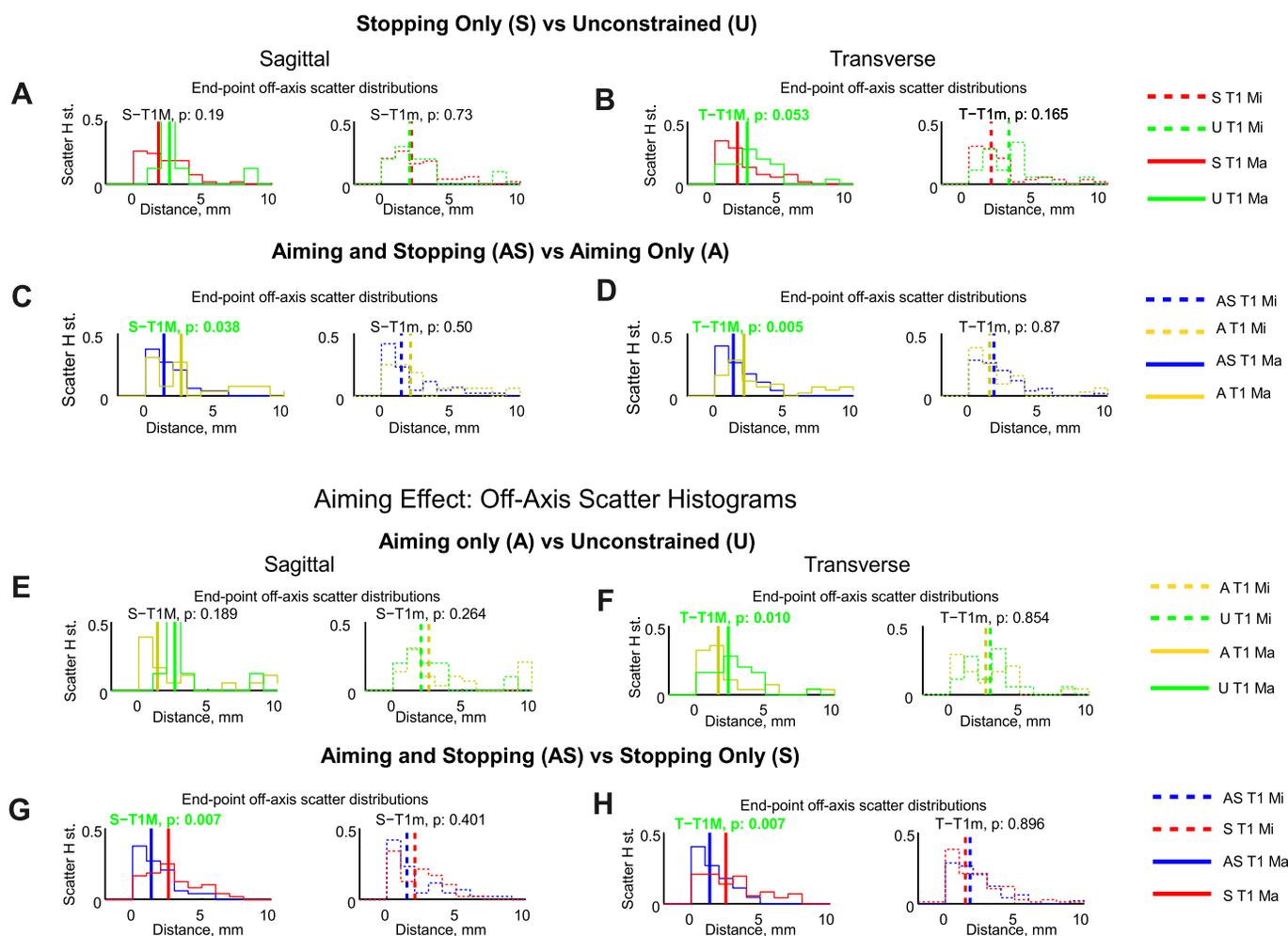


Fig. 7. Two cases of comparative analysis for the effect of aiming across subjects. *A–D*: stopping effect. In the *A* vs. *U* case, stopping at the target was not required in both cases; in the *AS* vs. *S* case, stopping at the target was required in both cases. *A* and *B*: off-axis end-point scatter distribution for the *A* vs. *U* experimental conditions for the sagittal (*left*) and transverse (*right*) arrangements. *C* and *D*: off-axis end-point scatter (cf. *left* drawing) distribution for the *AS* vs. *S* experimental conditions at each arrangement. *E–H*: aiming effect. The format was the same for the comparisons between aiming versus nonaiming constraint conditions.

and minor arrangements were much more significant (see the distance between solid and dashed preference curves in Fig. 8*B*). Therefore, if energy was the main factor influencing the subjects' choices, subjects should choose the same specific target at each arrangement independently of distance. However, as shown by the preference curves as a function of the relative target distance in Fig. 3, *A–D*, this was not the case. Although the major targets required less energy than minor targets, subjects still chose the minor target if it was much closer.

Nevertheless, although the main factor influencing the choices was the biomechanical ease of each movement, the different distances between major and minor sigmoids shown in Fig. 8*B* indicate that there was a different energy expenditure for the same arrangements across different constraint conditions. Although the horizontal distance between sigmoids was significant in all cases ($P < 0.01$), the size of that distance was largest when the stopping requirement was not enforced (*U* and *A* conditions), and it reduced whenever stopping was required (*AS* and *S* conditions). This suggests that the degree of control imposed by the requirement of stopping may, beyond kinematic differences, affect the transport energy with

which movements are executed and also modulate the subjects' target preferences. The degree of influence of energy in the control of movement and in the subjects' choices is analyzed further below.

Analysis of Muscle Contraction

As shown by the above results, the shift of preference for T_1 as a function of the control constraints demonstrates that factors related to the controllability of the arm exert an influence on decision making. Although the manner in which biomechanics and the strategy of control interact with one another is still a matter of further research, we can at least provide a partial account by investigating how muscle energy is expended to control movement along and perpendicular to the direction of movement, as a function of the control constraints considered in this study.

To this end, we performed a comparative analysis of the muscle contraction and muscle energy needed to perform the same movements as we varied the control constraints (see MATERIALS AND METHODS). Figure 9 shows the two components

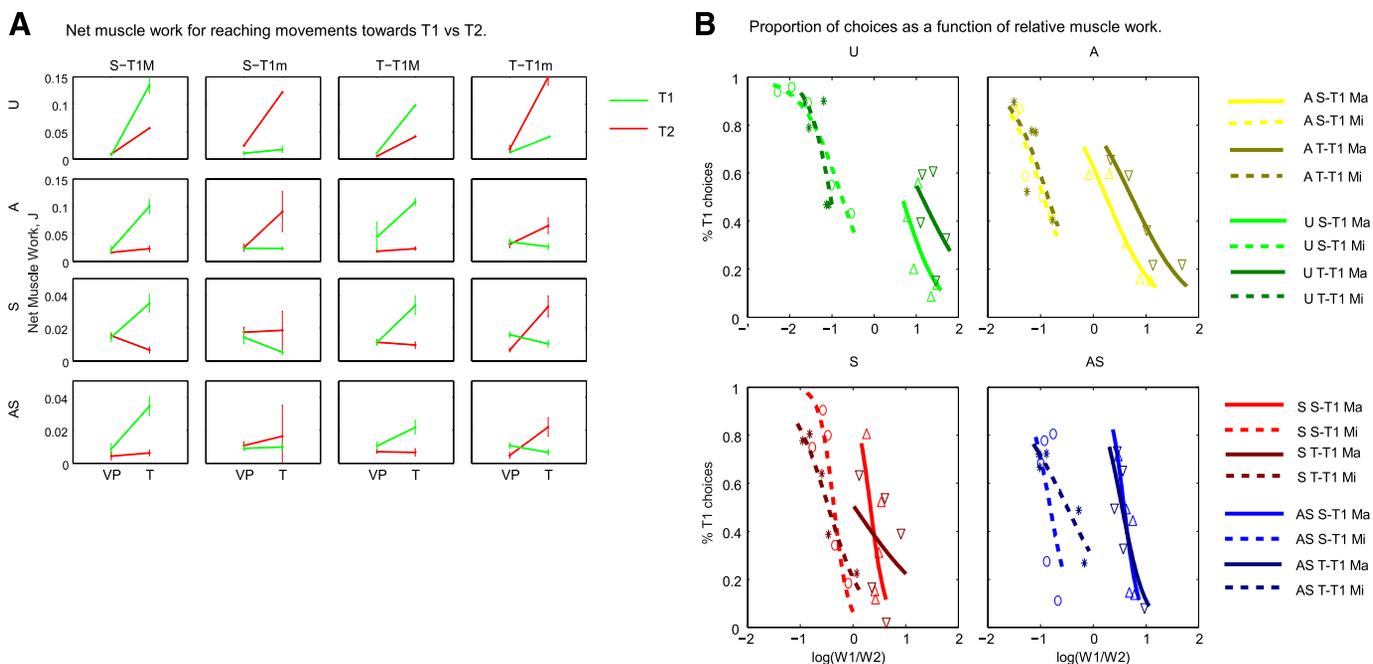


Fig. 8. *A*: energy between the origin and the VP and between the VP and the target (T) for each arrangement and control condition (U, A, S, and AS). *B*: proportion of choices as a function of relative muscle work (W_1/W_2) for each arrangement and condition. Note that the distance between major and minor curves was largest in the nonstopping conditions (U and A).

of muscle contraction, cocontraction (or WC) and UC, for each arrangement and constraint condition. The calculation was based on the procedure proposed by Thoroughman and Shadmehr (1999), although further normalization methods were necessary to equalize the kinematic disparities across conditions (see MATERIALS AND METHODS). Briefly, the goal of the normalization was to make it possible to quantify the cost of end-point stopping and aiming control constraints, which are otherwise confounded by the kinematic differences across conditions (see Fig. 4, *E* and *F*). To this end, we divided both metrics of contraction by the integral of the tangential velocity between movement onset and peak velocity to approximately equalize kinematics across conditions. Although the resulting contractions are rough estimates, they allowed us to have an approximate idea of the energy devoted to controlling the arm stability and to transport directly from the EMGs we recorded during each session. Subsequently, differences in those metrics across conditions should help to understand the level of influence of the constraints (aiming and stopping) in decision making between reaching movements. Not surprisingly, the level of normalized contraction increased as we gradually imposed control constraints (see the difference between the U and S curves and between the A and AS contraction curves in Fig. 9).

Furthermore, although we initially based our assessment on muscle contraction, we argue that these results may be extensible to muscle energy if we carefully assume (see MATERIALS AND METHODS) UC to be proportional to net muscle work during the movement. Although this ignores some significant components of UC that do not contribute to movement, we argue that the result could still provide the means to quantify the energy related to muscle cocontraction for the same movements. Although these are rough estimates, they may be an acceptable first-order approximation for the sake of analyzing the cost of each constraint condition (see MATERIALS AND METHODS for

further details). In this manner, we compared the contraction across conditions at four significant points along the trajectory: movement onset, the time the cursor enters the via point, the time the cursor enters the target, and movement offset (see Fig. 9) to quantify the cost of stopping and aiming. Typically, contraction scaled up from movement onset until reaching the target and decreased immediately after, indicating that the moment at which most control may be exerted is the time the cursor approaches the target. Furthermore, the differences between nonstopping and stopping conditions were very clear.

Typically, both WC and UC were larger at target arrival than during movement initiation and exhibited gradual increases as more control requirements were gradually imposed. Also, the percentage of contraction used to stabilize the end point varied significantly during movement, being maximal at the time of hitting the via point and during target approach: ~55% of the contraction was devoted to stopping and 12% was devoted to aiming. Overall, although these metrics are approximate, they strongly suggest an influence of the control requirements, with the control of the hand along the trajectory of movement being significantly more costly, in terms of energy, than in the direction perpendicular to it.

DISCUSSION

Decisions between concrete motor actions, such as turn right versus 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 analysis of a partic-

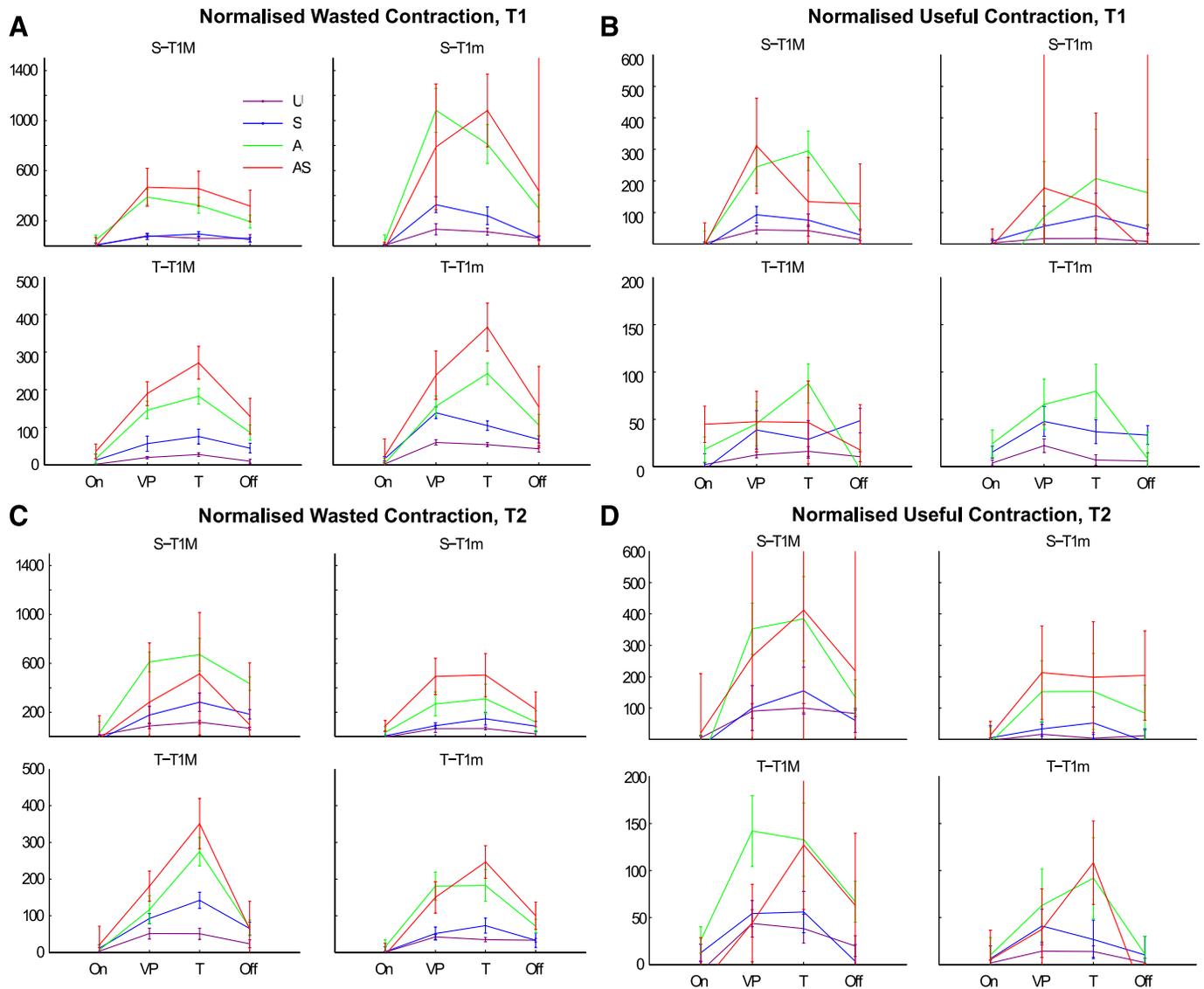


Fig. 9. Muscle contraction normalized by the integral of the transport energy between movement onset and the time of peak velocity: wasted contraction (A and C) and useful contraction (B and D). These functions of contraction were evaluated at four events during movement performance: movement onset (On), time of hitting the VP (VP), time of entering the target (T), and movement offset (Off). Graphs are shown for each geometric arrangement (sagittal T₁-M, sagittal T₁-m, transverse T₁-M, and transverse T₁-m) and are color coded according to the control condition (U, A, S, and AS). Note that, in most cases, there was a significant difference ($P < 0.05$ by KS test) between the levels of contraction at the time of crossing the VP and of entering the target between those conditions in which stopping was required (AS and A) and those in which stopping was not required (U and S). A: normalized wasted contraction for movements toward T₁. B: useful contraction for movements toward T₁. C: normalized wasted contraction for movements toward T₂. D: useful contraction for movements toward T₂.

ular choice as well as its likelihood of success. With this view in mind, this report analyzed how certain aspects of actions, such as biomechanical ease and controllability, influence human reaching choices.

In a previous study (Cos et al. 2011), we showed that biomechanical properties of candidate actions strongly influence the decision between them. Here, we further showed 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 T₁ major and T₁ minor preference curves) was observed in the most unconstrained case (U condition). Furthermore, the largest reduction of the biomechanical effect was exerted by the constraint of stopping

at the target. As shown by the comparison between the AS and A conditions in Fig. 5, C and D, the preference for the major target is weaker when stopping is required. Furthermore, although the targets are narrow in both cases, the off-axis end-point scatter at the target is significantly reduced when stopping is enforced. This is consistent with the end point moving along the direction of maximal mobility being less energy demanding and the easiest to direct. However, this may make stopping more difficult, making the major target less desirable and increasing the need for precise control, resulting in the reduction of end-point scatter when stopping is enforced. On the other hand, movement to minor targets naturally exhibits a wider end-point scatter, which does not diminish when stopping is enforced. In a similar fashion, although to a much lesser extent, the aiming constraint also tends to reduce the effect of biomechanics (see the comparison between A and U

cases in Fig. 6, *A* and *B*) and to reduce the off-axis scatter. Although this is partly due to the reduction of the target width, the fact that this reduction is only significant for the major targets suggests that the major cause is the aiming requirement. 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.

Furthermore, the results shown above demonstrate that there is an interaction between the intrinsic properties of the arm and the degree of control demanded by the surrounding environment as factors that may influence the selection of motor actions. Moreover, the differences obtained as a function of the degree of control demanded by the task context provide an affirmative answer to the question of whether each of these factors is involved in the process of decision making. It is easy to picture natural situations in which the prediction of the degree of controllability of any given movement is going to be important for selecting among complex actions. For example, a tennis player who has to quickly decide whether to use their forehand or backhand may gain some advantage if able to predict not only the biomechanical cost but also the control demanded by these movements and, consequently, their chances of success. Neurophysiological data have suggested that the brain can simultaneously specify different courses of action in sensorimotor cortical areas (Cisek and Kalaska 2002, 2005; McPeck and Keller 2002; Baumann et al. 2009), and it has been suggested that these representations compete for overt execution (Cisek 2007; Cisek and Kalaska 2010; Pastor-Bernier and Cisek 2011). As decision-making variables are computed and gradually fine tuned, they can bias the competition in favor of the "better" choice. Our data suggest that this bias includes information about the biomechanical properties of the motor apparatus as well as about the difficulty of controlling a given movement and that both of these are at least partially estimated before movement onset.

Transport Energy

Although some recent experiments have claimed that the central nervous system does not minimize energy cost in arm movements (Kistemaker et al. 2010), several other studies have suggested its implication during movement planning and execution (Alexander 1997; Engelbrecht 2001; Guigon et al. 2007; Shadmehr 2010). In our case, the experimental setup was designed to equalize launching biomechanics and energy and to maximize the difference between the biomechanical ease of arriving at the two targets. However, energy significantly covaries with biomechanics; thus, the difference of biomechanics at the target will also translate to a difference of energy cost between reaching movements. To disambiguate between these, we performed an additional analysis by calculating the subjects' target preference as a function of the relative muscle work to reach each target (see Fig. 8*B*). Remarkably, the range of variation of muscle work as a function of relative target distance within the same arrangement was very narrow, thus yielding close to vertical T_1 preference curves. In fact, the energy cost differences between movements were always larger for the major target than for the minor target within each

arrangement. If energy were the only factor of the subjects' choices, then subjects should always have chosen the major target independently of the relative target distance. However, they did not, and target distance determined choices when the difference was large, as shown by the subjects' preference curves in Fig. 3, *A–D*. This confirms that while energy is an important factor influencing the process of decision making, it is not the only one.

Energy, Biomechanics, Impedance Modulation, and Control of Movement

Although both aiming and stopping constraints do not equally affect the subjects' target preference, off-axis scatter distributions at the target are consistently dependent on these constraints. In other words, the off-axis scatter for T_1 or T_2 in their major configuration is significantly smaller ($P < 0.05$ by KS test) when stopping is enforced (see distributions in Fig. 7). Likewise, the mean variability diminishes along the same T_1 major directions when aiming is enforced. However, the same scatter distributions do not exhibit any significant sensitivity to the control constraints for T_1 minor targets, meaning that despite the additional level of control, this does not affect the end-point variability along these directions.

The arm is naturally least sensitive to perpendicular perturbations when it is moving along the direction of maximal mobility/admittance. We conjecture that when constraints are applied, the reduction of variability along those directions is a consequence of biomechanics. In other words, the directions of maximal mobility/admittance may be viewed as valleys in a dynamic landscape that facilitate end-point stability perpendicular to movement direction and, as more control constraints are applied, the reduction of end-point variability becomes more significant. Movements along the minor axis exhibit a larger variability because of the lack of mechanical stability along the perpendicular direction. In other words, it is equivalent to moving along a ridge in the dynamic landscape and, hence, is most sensitive to perpendicular perturbations. On these grounds, we argue that since the movement along the minor direction is intrinsically more variable, the operation of additional control mechanisms yields a similar distribution of end-point scatter across constraint conditions. This is consistent with the results of Lametti and Ostry (2010), who showed that end-point error varies as a function of arm stiffness.

Admittedly, we had expected that decisions between motor actions would be guided toward directions of lesser variability, as the decrease of variability is typically associated with more effective control. However, subjects less frequently selected major targets as the stopping or aiming constraints were applied and the variability was smaller. This suggests that there are additional criteria, presumably subjective comfort, guiding the subjects' choices in addition to biomechanics.

Each constraint condition implies clear differences of energetic cost. We argue that an estimate of this cost is predicted before movement onset and modulates the relative subjective desirability of each candidate movement. To further investigate the energetic demands of each constraint, we analyzed normalized WC and UC (Thoroughman and Shadmehr 1999). We assumed that UC was a rough approximation of the muscle work expended to perform the movement, while WC was associated with its control and stability. Although these metrics

are merely rough estimates, they provide a qualitative description of how energy is expended to control movement under each constraint condition. Note that since the time to reach the target was significantly different across constraint conditions, our conclusions are based on a comparison at four critical points along the trajectory: movement onset, time of crossing over the via point, time of entering the target, and movement offset (see Fig. 9). As shown, both WC and UC increased from the lowest level for the baseline U case until the largest values when both constraints were applied (AS case). The trend was that both contraction metrics exhibited a tendency to gradually increase until the time of entering the target and decrease until the offset of movement.

Finally, we also calculated WC and UC during the launching and arrival intervals. Importantly, both values of contraction did not significantly vary between launching and arrival for the U and A conditions but did change very significantly for the S and AS conditions. This indicates that the need of stopping at the target increases the energy demand by ~50% during target arrival. Furthermore, the fact that as constraints were added the subjects' target preference toward the major targets was reduced suggests that there is some advantage to applying control over the end point along the minor direction. In conclusion, this suggests a trade off between the advantages provided by moving along directions of lower inertia and being able to apply control along the direction of movement while maintaining the trajectory stable (along the directions of larger inertia).

While we cannot rule out some effect of learning on the effects described here, the results of our analyses suggest that the subjects' target preference already reflected the effect of biomechanics after a few trials and did not significantly vary during the experimental session. It is reasonable to assume that the subjects have extensive practice with reaching movements throughout their lives and that, consequently, they were capable of estimating biomechanical and control costs before onset for these relatively easy reaching movements. Thus, if there was an effect of learning, it should have been minimal.

Conclusions

In summary, our results reveal that the requirement of a controlled stop at the target or of precise aiming at a small target both reduce 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 that may be predicted and can influence the selection of a movement.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: I.C. and P.C. conception and design of research; I.C. and F.M. performed experiments; I.C. and F.M. analyzed data; I.C., F.M., and P.C. interpreted results of experiments; I.C. prepared figures; I.C. and P.C. drafted manuscript; I.C., F.M., and P.C. edited and revised manuscript; I.C., F.M., and P.C. approved final version of manuscript.

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