The influence of predicted arm biomechanics on decision making

Ignasi Cos, Nicolas Bélanger, and Paul Cisek
Département de Physiologie, Université de Montréal, Montréal, Québec, Canada

Cos I, Bélanger N, Cisek P. The influence of predicted arm biomechanics on decision making. *J Neurophysiol* 105: 3022–3033, 2011. First published March 30, 2011; doi:10.1152/jn.00975.2010.—There is considerable debate on the extent to which biomechanical properties of movements are taken into account before and during voluntary movements. For example, while several models have described reach planning as primarily kinematic, some studies have suggested that implicit knowledge about biomechanics may also exert some influence on the planning of reaching movements. Here, we investigated whether decisions about reaching movements are influenced by biomechanical factors and whether these factors are taken into account before movement onset. To this end, we designed an experimental paradigm in which humans made free choices between two potential reaching movements where the options varied in path distance as well as biomechanical factors related to movement energy and stability. Our results suggest that the biomechanical properties of potential actions strongly influence the selection between them. In particular, in our task, subjects preferred movements whose final trajectory was better aligned with the major axis of the arm's mobility ellipse, even when the launching properties were very similar. This reveals that the nervous system can predict biomechanical properties of potential actions before movement onset and that these predictions, in addition to purely abstract criteria, may influence the decision-making process.

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

IT IS WELL KNOWN that simple point-to-point reaching movements tend to minimize distance, producing a straight path (Morasso 1981), at least for small amplitudes. However, as trajectories extend over larger regions of space or the task complexity increases, factors other than kinematics, such as arm anisotropies, passive inertial properties, and muscle viscoelastic properties, become increasingly relevant (Gordon and Ghez 1987; Flash 1987; Vindras et al. 2005; Guigon et al. 2007). This suggests that movement planning may take into account the intrinsic properties of the limb (Soechting and Lacquaniti 1981; Kaminski and Gentile 1989), perhaps even including implicit knowledge about dynamics (Uno et al. 1989). It remains difficult, however, to distinguish what is planned ahead of movement onset and what is the result of feedback control during execution.

Evidence that planning includes predictive computation of biomechanical factors comes from studies of movements around obstacles. For example, Sabes and Jordan (1997) and Sabes et al. (1998) studied how subjects' reaching trajectories around a pointed object varied as a function of how their body was oriented with respect to that object. They found that trajectories were curved so as to be mechanically most resistant to potential perturbations at the point closest to the tip of the obstacle, independently of kinematic factors. This demonstrated that arm morphology and its impedance parameters influence the planning of the trajectory together with the geometry of the environment. In the language of optimal feedback control theory (Todorov and Jordan 2002), this suggests that arm biomechanics may be a factor in the cost function used to plan each part of the movement. Again, however, the question remains whether biomechanics were taken into account before movement onset or whether their influence emerged online.

Here, we aimed to extend these findings and asked whether biomechanical factors are taken into account during the process of deciding between two different potential movements. In particular, we analyzed situations in which subjects were presented with two potential reaching movements, each with different biomechanical properties, and were asked to freely choose between them. To characterize the effects of biomechanics, we considered different aspects of the arm's biophysical properties: its morphological anisotropies, its distribution of mass and of viscoelastic properties (Hogan 1985a, 1985b, 1985c), and metabolic cost (Alexander 1997; Guigon 2010). Under which conditions are each of these factors more influential? One might expect that the same parts of the brain involved in trajectory planning and control may also actively participate in the choices among different movements (Cisek 2007; Cisek and Kalaska 2010), and if those regions are sensitive to biomechanics, then so should be the choice. For example, suppose two movement options are simultaneously represented in frontoparietal regions, as suggested by neurophysiological studies (Glimcher 2002; Cisek and Kalaska 2005; Gold and Shadlen 2007). Their biomechanical costs could be predicted by a forward model, possibly residing in the cerebellum (Hua and Houk 1997; Pasalar et al. 2006; Bastian 2006), and used to bias movement selection. If so, then choices should reflect an implicit knowledge of biomechanical factors in addition to any influences of visual factors, such as relative path length. This would have two important implications. First, it would demonstrate an intimate integration between action selection and movement planning mechanisms. Second, it would demonstrate that the central nervous system possesses at least implicit knowledge of biomechanics before movement onset, which it can make use of while still making a decision.

MATERIALS AND METHODS

Characterization of biomechanics. There is a variety of biomechanical factors associated with a given movement, including interaction torques, passive inertial and muscle viscoelastic properties, or more elaborate factors dependent on joint kinematic and dynamic factors, such as muscle energy. Because our primary interest here was to determine whether any of these factors can be estimated before movement onset and influence decision making, we sought a simple metric for distinguishing movements according to their general "bio-

mechanical ease." To this end, we used the concepts of 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 the elastic properties of the arm. As we did not alter normal dynamics (i.e., no perturbations or external force fields were applied), we assumed that mobility and admittance covaried to a large extent and that estimating one can yield an estimate of the other. On the plane, mobility can 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. As both metrics covary, mobility and admittance axes approximately align. Because the factor of biomechanics is the degree of alignment with the major axis of two aligned ellipses, we simplified by calculating the end-point mobility, as described by *Eq. 1*:

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

The mobility tensor $W(\theta)$ is the inverse of the inertia tensor $I(\theta)$. *Equation 1* transforms the mobility tensor from joint space into end-point space using the Jacobian $J(\theta)$ of the arm. Since measures of arm inertia are not directly available, we used a planar two-segment model of the arm, which describes each segment as a center of mass, m_s and m_e, located at a fraction c_s or c_e, along the respective segment length [shoulder (subscript "s") or elbow (subscript "e")]. *Equation 2* shows the resulting formulation of $I(\theta)$:

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

In *Eq. 2*, θ_s and θ_e are the shoulder and elbow angles, as shown in Fig. 1*B*, and l_s and l_e are the arm segment lengths. The remaining parameters are averaged mass and mass center distances, which have the following average values: $m_s = 1.76$ kg, $m_e = 1.65$ kg, $c_s = 0.475$, and $c_e = 0.42$ (Sabes and Jordan 1997).

The matrix $W(\theta)$ can be visually represented as an ellipse. Trajectories that are aligned with the major axis of this ellipse are considered to be biomechanically easier than trajectories that are aligned with its minor axis. Thus, the alignment of a given trajectory with the ellipse will be used as our metric for defining biomechanical ease.

Although here we only calculate the ellipse of mobility, we do not assume that mobility was the only factor of biomechanics exerting an influence on movement preparation and decision making. We acknowledge that biomechanics also include other factors, such as the muscle energy required for moving along a given trajectory. However, we view all of these as consequences of the arm's biophysical properties, which tend to covary with each other. Thus, although we chose to characterize differences in biomechanics using a simple metric that captured the anisotropy of biophysical properties of the arm (i.e., as mobility), this is not meant to imply that we conclude that mobility is the single variable of interest to the nervous system. Instead, we suggest that the system takes biomechanical anisotropies into account and that mobility is a convenient metric for characterizing these anisotropies. Mobility may be calculated in a straightforward fashion and provides an easily interpretable visual representation in the form of an ellipse. For the design of our experimental setup, we used the alignment of the trajectory with the major or minor axis of the ellipse as a metric that characterizes the biomechanical ease of the trajectory. Our experimental paradigm was designed to simultaneously vary both visual factors (trajectory path length) and biomechanical factors (alignment of the trajectory with the axes of the mobility ellipse) to study their effects on subject response choices. The impacts of additional factors such as interaction torques and muscle energy have been individually addressed via control experiments (see Supplemental Material).[1]

Subjects. Twelve right-handed subjects (7 women and 5 men, average age: 29 yr) participated in this study. They had no known

---

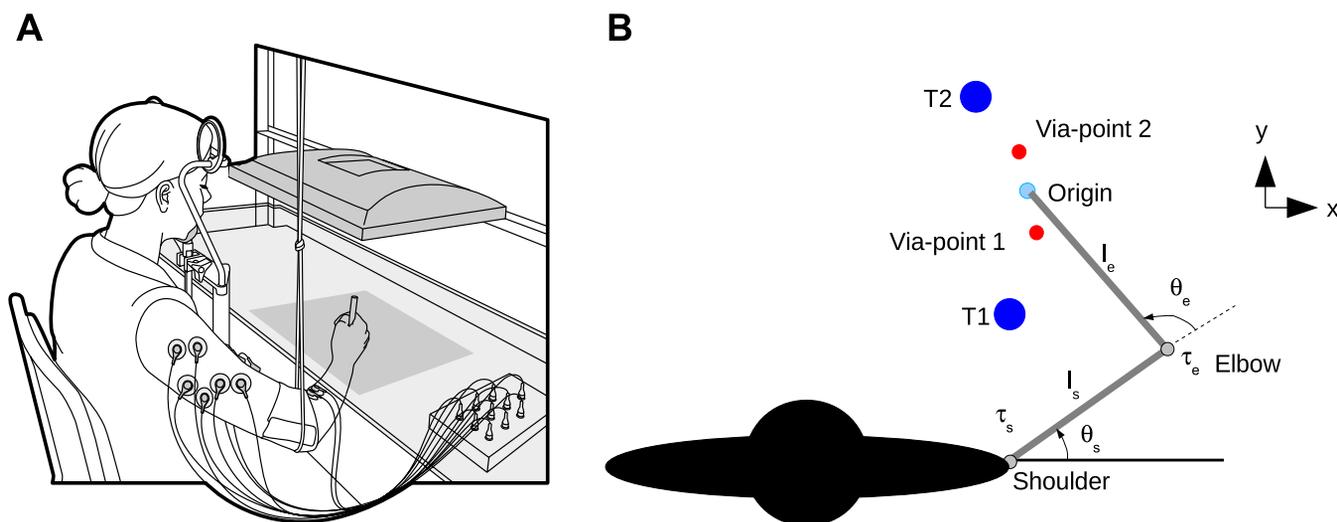[1] Supplemental Material for this article is available at the *Journal of Neurophysiology* website.

Fig. 1. Experimental setup and schematic of the basic geometric arrangement. *A*: depiction of the experimental setup. The subject sits on a chair in front of a digitizing tablet with electromyographic surface electrodes attached to the main muscle groups of the upper arm. Stimuli and cursor feedback are projected onto a mirror placed between the table and the monitor. *B*: model of the experimental setup. The right arm was modeled as a two-segment rigid body rotating around the shoulder and elbow joints. θ_s and θ_e are the shoulder and elbow angles, respectively, and l_s and l_e are the upper arm and forearm lengths, respectively. The geometric arrangement is defined by an origin (cyan circle), via points (red circles), and *targets 1* and *2* (T1 and T2; blue circles). τ_s and τ_e are the shoulder and elbow torques, respectively.

neurological disorders and had normal or corrected to normal vision, and all were naïve about the purpose of these experiments. They all signed a consent form before the experimental session was initiated, and the protocol was approved by the Human Research Ethics Committee of the Faculté de Médecine, Université de Montréal.

Task apparatus. The task apparatus consisted of a digitizing tablet (GTCO Camcomp IV, 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. 1*A*). Subjects made movements using a digitizing stylus whose position was sampled at 125 Hz with a spatial resolution of 0.006 in. $\pm$ 0.127 mm.

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), bandpassed 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 in a PC running Windows XP (Microsoft, Redmond, WA). Maximum force was estimated at the beginning of each task for each 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 session were transferred to a MySQL database (Sun Microsystems, Santa Clara, CA) for further analysis using custom-designed Matlab scripts (Mathworks, Natick, MA).

The subject was required to maintain posture at a fixed distance from the digitizing tablet and to place his/her chin on the chinrest. To diminish fatigue, the right arm was suspended in a loose brace wrapped around the subject's elbow, to which a rope was attached from a sling hung above the digitizing tablet. To diminish the pendulum effect, the length of the pendulum was the longest possible (1.5 m above the digitizing tablet).

The subject was instructed to hold the stylus with the right hand, to maintain its orientation vertical at all times, and not to bend the wrist. The experimenter visually monitored the experiment to ensure that the subject complied with this requirement.

Behavioral task. Each experimental session consisted of 1,200–1,800 reaching trials of two types: two target (600–900 trials) and one target (600–900 trials). Within each trial, each potential reaching path was defined by the origin cue (cyan circle, radius: 1 cm), a via point (red circle, radius: 1 cm), and a target (dark blue circle, radius: 2 cm; see Fig. 1*B*). The geometry of the arrangements was the same for all 12 subjects. However, for the first seven sessions, the location of the target cues was indicated by two acute triangles, each pointing toward a circular target region whose border was not explicitly displayed. In subsequent sessions, we eliminated the triangles and made the target regions visible (as blue circles) to avoid potential visual effects caused by the triangles. The analysis of data obtained with both types of stimuli yielded the same target preferences, and, therefore, we collapsed the data from both sets into a single set (see RESULTS). Each trial began when the origin cue was shown on the screen and the subject moved the stylus into it. After the stylus had been held there for a 300- to 700-ms center hold time, the stimuli defining both potential trajectories were shown. After a 500- to 700-ms observation time, a "go" signal was given (origin cue disappeared). Subjects were instructed to react as fast as possible, to choose the movement that seemed most comfortable, and to move the stylus over the via point and then stop within the target cue for a 500-ms target hold time (THT). If the subject did not manage to maintain position within the target for 500 ms, the color of the target changed to purple. However, subjects were instructed that this change of color was only for informative purposes; thus, although they should try to maintain position at the target during THT, leaving before then was not considered an error. This was told to the subjects so that they did not avoid attempting to reach targets for which their accuracy was low. A trial was only considered an error if the stylus left the origin before the go signal, if the reaction time (RT) was shorter than 200 ms or longer than 1000 ms, or if the stylus reached the target before first crossing over the via point. If a trial was an error, it was not repeated. Trials in which the subject crossed the via point but failed to enter the target or failed to stop at the target during the THT time were used for further analysis. Those 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 moved over them.

Manipulation of visual versus biomechanical factors. The goal of the experiment was to analyze subjects' preferences as a function of relative path distance and arm biomechanics. In two-target trials, we placed the via points and targets such that the total path lengths to *target 1* (T1) versus *target 2* (T2) were either 9 versus 13 cm (20% of trials), 10 versus 12 cm (20%), 11 versus 11 cm (20%), 12 versus 10 cm (20%), or 13 versus 9cm (20%). All other things being equal, one would expect that subjects should prefer shorter movements (Guigon et al. 2007), which reach lower peak velocities and have lower variability. However, we also manipulated the biomechanical factors associated with each potential movement by placing the via points and targets such that the cursor would arrive at the target along a trajectory that was either aligned with the major or the minor axis of the ellipse (as noted above, we used the alignment of the mobility/admittance ellipse with the trajectory as a metric of biomechanical anisotropy). In two-target trials, one of the trajectories would always arrive along the major axis, whereas the other would arrive along the minor axis; thus, the biomechanical costs of the trajectories would be very different even if the path distances were the same. Furthermore, the via points were always placed in opposite directions from the origin, so that the launching part of each trajectory would be similar in terms of biomechanics. In summary, we presented subjects with four types of target arrangements (Fig. 2, *A* and *C*) classified according to their overall orientation (transverse or sagittal) and according to their arrival biomechanics to T1 (e.g., T1 major or T1 minor). For each of the four types of arrangements, we used the five relative distances mentioned above. For the sagittal arrangements (Fig. 2*A*), the lower target was denoted as T1, and for the transverse arrangements (Fig. 2*C*), the rightmost target was T1. Thus, in the arrangement shown in Fig. 2, *A* and *C*, *left*, which we call the T1 major condition, reaching movements to T1 would arrive on a path aligned with the major axis of the mobility ellipse, whereas movements to T2 would arrive on a path aligned with the minor axis. In contrast, in the T1 minor arrangement shown in Fig. 2, *A* and *C*, *right*, movements to T1 would arrive along the minor axis and movements to T2 would arrive along the major axis.

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 spatially 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, T1 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 T1 or T2 in each of the two (sagittal or transverse) arrangements but would not vary between the T1 major and T1 minor conditions.

Interspersed among the two-target trials were one-target trials. They were included for three main reasons: to mitigate habits (see below), to enforce practice of all targets independently of a subject's preference, and to provide accuracy data at the target for each potential trajectory type.
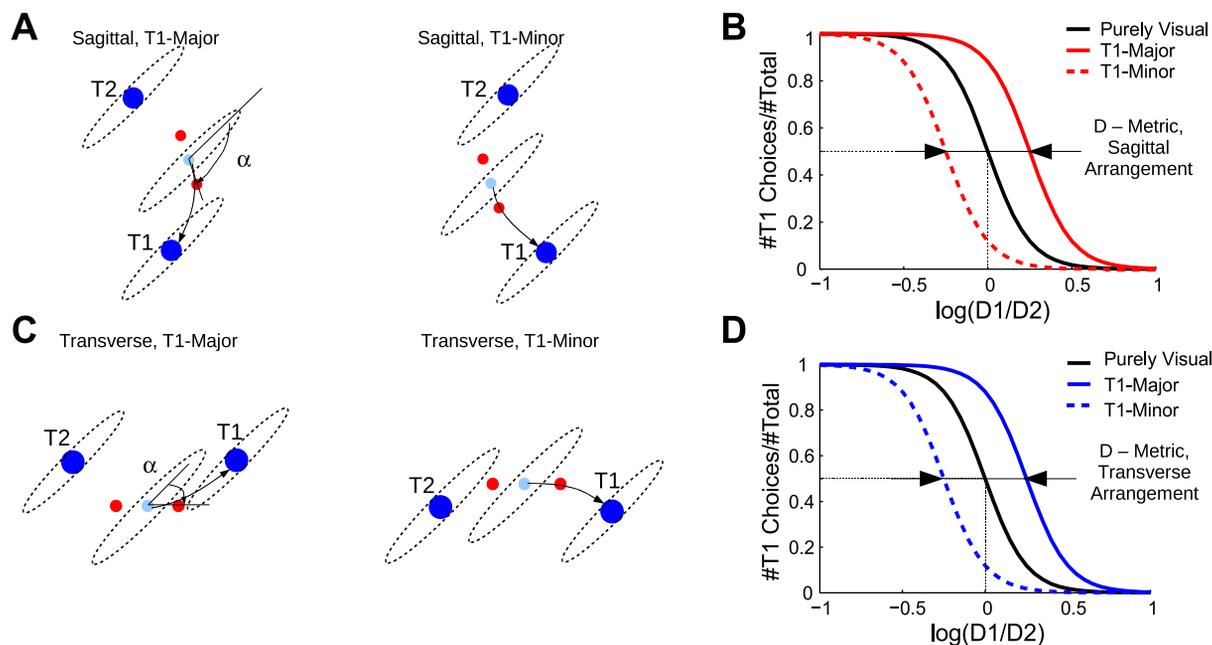
Fig. 2. "Sagittal" (S) and "transverse" (T) planar stimulus arrangements for the case of equal relative origin-target distance and predicted effects of arm biomechanics on decision making. *A*: depiction of the sagittal arrangements (angle α: $-135°$). The ellipses centered at the origin and targets show a qualitative display of the arm mobility/admittance at those locations. Note that the arrival trajectory to T1 or T2 is opposite in terms of alignment with the axes of that ellipse. In the "T1 major" arrangement, the trajectory to T1 is aligned with the major axis of the ellipse while the trajectory to T2 is aligned with its minor axis. The opposite is true for the "T1 minor" arrangement. *B*: predicted T1 preference curves (*y*-axis) for each sagittal arrangement plotted as a function of the relative origin-target distance (*x*-axis). If the decision is purely based on visual criteria, the selection policy should favor the closest target more often, yielding an equal proportion of choices at equal relative distance between targets (black sigmoid). However, if arm biomechanics influence the decision, then the preference curve for the T1-major arrangement (solid sigmoid) should be shifted to the right of the T1-minor arrangement preference curve (dashed sigmoid). We used the *D* metric to quantify this influence (the distance between the sigmoids at each arrangement for *y*-axis equal to 0.5). *C*: depiction of the transverse arrangement (angle α: $-45°$). *D*: predicted T1 preference curves for the transverse arrangements.

Mitigating the effect of habits. Because we were interested in investigating how biomechanics 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 either in an approximately sagittal (Fig. 2*A*) or transverse orientation (Fig. 2*C*), each with either the T1 major or T1 minor configurations. This made it equally probable on any given trial that the easier movement would begin in one of the four cardinal directions. Second, we varied the precise angle (α) between the major axis of mobility and the via points such that it was -120, -135, or $-150°$ for the sagittal arrangement or -30, -45, or $-60°$ for the transverse arrangement (subjects performed a minimum of 15 trials of each type). This further increased the directional uncertainty within the sagittal or transverse arrangements while maintaining the similarity of their biomechanics across the three possible values of α. Third, we interspersed two-target trials with one-target trials corresponding to each of the eight possible trajectories shown in Fig. 2, *A* and *C* (path length of 11 cm only). This forced the 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. It is expected that path length significantly influences the choice of target, with closer targets tending to be selected more often when all else is equal. Since we had a set of five possible relative T1/T2 distances for different trials, we can plot the proportion of trials for which subjects chose T1 over the total number of choices to obtain a measure of each subject's preference for T1 as a function of the relative distance to the two targets. The proportion of T1 choices (P_{T1}) for each configuration (sagittal T1 major, sagittal T1 minor, transverse

T1 major, and transverse T1 minor) was plotted on a logarithmic scale and fitted with a sigmoidal curve, as described by *Eq. 3*:

$$P_{T1}(Q) = \frac{\exp(Q)}{1 + \exp(Q)}; \ Q = a \times \log\left(\frac{D_1}{D_2}\right) + b \qquad (3)$$

where Q is, *a* and *b* are the parameters fitted for data from each configuration, and D_1 and D_2 are the distances to T1 and T2, respectively, measured along the path from the origin through the via point and to the target. If choices were only based on path distance, these preference curves should be similar in both T1 major and T1 minor conditions for the sagittal and transverse arrangements. However, if subjects take biomechanics into account, then we should observe biomechanics-dependent shifts in the preference curves. Figure 2, *B* and *D*, shows the predicted results. If biomechanics have any effect at all, it should increase or decrease the proportion of T1 choices as a function of the alignment of the trajectory approaching T1 with the mobility ellipse at T1.

In particular, we predicted that the preference curve for the T1 major configuration should be shifted to the right of the curve for the T1 minor configuration and that this should be observed in both the sagittal (Fig. 2*B*) and transverse target orientations (Fig. 2*D*). To determine the significance of the shift, 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 T1 major versus T1 minor configurations at a *y*-value of 0.5. We call this metric *D* (see Fig. 2, *B* and *D*). 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 5 relative distances were randomly shuffled between major versus minor configurations. If the value of *D* was larger than 95% of the distance values obtained from shuffled data, the result was considered significant at $P < 0.05$.

Interaction torques. The geometric arrangements shown in Fig. 2, *A* and *C*, were designed to maximize the difference in the alignment of the axes of the mobility/admittance ellipse with the trajectory as the hand approached the target. However, interaction torques between joints may also influence the selection between targets independently of mobility, even though the path lengths of each trajectory are relatively short (~10 cm). An EMG study (Gribble and Ostry 1999) has revealed that motor commands compensate for torques resulting

from intersegmental dynamics, and it is plausible that such anticipation may also influence the selection of one trajectory over another.

To investigate whether interaction torques influenced choices, we assessed their contribution to the total muscle torques within the sagittal and transverse arrangements. We calculated the interaction torques (τ_{it}) using *Eq. 4* (Gribble and Ostry 1999) and the muscle torque contribution (τ_m) by subtracting the interaction torques from the total joint torques (τ_t) (*Eqs. 5* and *6*), as follows:

$$\tau_{it} = \begin{bmatrix} 0 & \mathbf{I}_{12} \\ \mathbf{I}_{21} & 0 \end{bmatrix} \begin{bmatrix} \theta_s \\ \theta_e \end{bmatrix} + \begin{bmatrix} -m_e l_s l_e \sin(\theta_e)\dot{\theta}_e & -0.5 m_e l_s l_e \dot{\theta}_e \sin(\theta_e) \\ 0.5 m_e l_s l_e \dot{\theta}_s \sin(\theta_e) & 0 \end{bmatrix} \begin{bmatrix} \dot{\theta}_s \\ \dot{\theta}_e \end{bmatrix} \quad (4)$$

$$\tau_t = \mathbf{I}(\theta)\dot{\theta} + \mathbf{C}(\dot{\theta}, \theta)\dot{\theta} \quad (5)$$

$$\tau_m = \tau_t - \tau_{it} \quad (6)$$

where $\dot{\theta}$ is the joint velocity vector. The joint torques may be obtained from the inverse dynamics equation of a two-segment rigid body arm restricted to planar motion. Within these conditions, $\mathbf{I}(\theta)$ is the inertia tensor, as defined by *Eq. 2*, and $C(\dot{\theta}, \theta)$ is the tensor of centrifugal and Coriolis forces, defined by *Eq. 7* (Gribble and Ostry, 1999):

$$\mathbf{C}(\dot{\theta}, \theta) = \begin{bmatrix} 2l_s m_e r_e \sin(\theta_e)\dot{\theta}_s & m_e r_e l_s (\dot{\theta}_s + \dot{\theta}_e) \sin(\dot{\theta}_e) \\ m_e l_s l_e \dot{\theta}_s \sin(\theta_e) & 0 \end{bmatrix} \quad (7)$$

Angles θ_s and θ_e are the shoulder and elbow angles, as shown in Fig. 1*B*, and r_e is the distance from the elbow joint to the center of mass of the lower arm segment. The remaining parameters are the arm segment masses ($m_s = 1.76$ kg and $m_e = 1.65$ kg) and arm segment lengths ($l_s = 31$ cm and $l_e = 32$ cm).

Muscle work. 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 point positions within each arrangement. The muscle work (*W*) to move the arm from *point A* to *point B* may be calculated by integrating muscle torques between both points, defined in angular coordinates, as in *Eq. 8*:

$$W = \int_A^B \tau_m d\theta \quad (8)$$

Path curvature. Since we wanted to have a metric of curvature independent of velocity to avoid local singularities, we opted for using the metric *K*, which is the sum of the perpendicular distances from each point along the trajectory to its corresponding projection onto the straight line between the initial and final positions, normalized by the distance between the origin and the target (Torres and Andersen 2006). A value of $K = 0$ would indicate a perfectly straight trajectory.

Movement onset, movement offset, and RTs. We detected the time of movement onset by determining the moment at which either the *x*- or *y*-coordinate of the cursor 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 cursor position did not differ from its previous value for more than 50 ms after the stylus entered the target. We defined RT as the interval between the go signal and the movement onset.

RESULTS

Choice preferences. To assess the effect of biomechanics on subject choices, we calculated the preference curves with respect to T1 (see MATERIALS AND METHODS) for each of the four arrangements. These are shown in Fig. 3*A* for two typical

subjects as well as for grouped data from all subjects. As expected, there was a significant influence of path distance on the choice of target, with T1 chosen more often when it was the closer of the two targets. If the selection criterion were purely visual, the preference for either target would be similar regardless of whether it is approached along a major or minor trajectory. However, the curves exhibited statistically significant shifts, which suggests that choices are influenced by arm biomechanics. As predicted, the curve for the T1 major condition was shifted to the right of the curve for the T1 minor condition ($P < 0.05$, bootstrap test), indicating that in the T1 major condition, T1 is often more appealing than T2 even when its distance from the origin is larger. In all of these geometric arrangements, the subject's preference was for the target whose approach trajectory was aligned with the major axis of the end-point mobility/admittance ellipses. This suggests that, in addition to path length, the selection process is also influenced by biomechanical factors such as sensitivity to potential perturbations or required energy. We calculated the target preference for all 12 subjects and found statistically significant effects ($P < 0.05$, bootstrap test) in 12 of 12 subjects for the transverse configuration and in 9 of 12 subjects for the sagittal configuration.

RTs and error rates. Half of the subjects exhibited significant differences between RTs for reaching movements toward major versus minor targets. Typical RTs from one-target trials varied within a range of 450–800 ms (SD: 250 ms). Figure 3*B* shows the RTs for two subjects as well as averaged across all subjects. Differences between RT distributions were statistically significant [$P < 0.05$, Kolmogorov-Smirnov (K-S) test] for reaching movements toward major or minor targets in 6 of 12 subjects. A comparison between RT distribution for reaches toward T1 and T2, independently of major versus minor, showed that differences were nonsignificant in 8 of 12 subjects (e.g., see Fig. 3*B, left*). This may indicate that the biomechanics associated with minor movements require more extensive preparation than major movements.

As we were concerned that the subjects' choices may be biased by differences in performance between movements, we performed a comparative analysis of error rates between major and minor reaching movements (K-S test). The trials considered for analysis were those in which the end point left the origin after the go signal and crossed over the via point. In addition to this, correct trials were those in which the end point entered the target and held position at the target during the THT. Error trials were those in which the end point missed the target or failed to maintain position at the target during the THT. The K-S
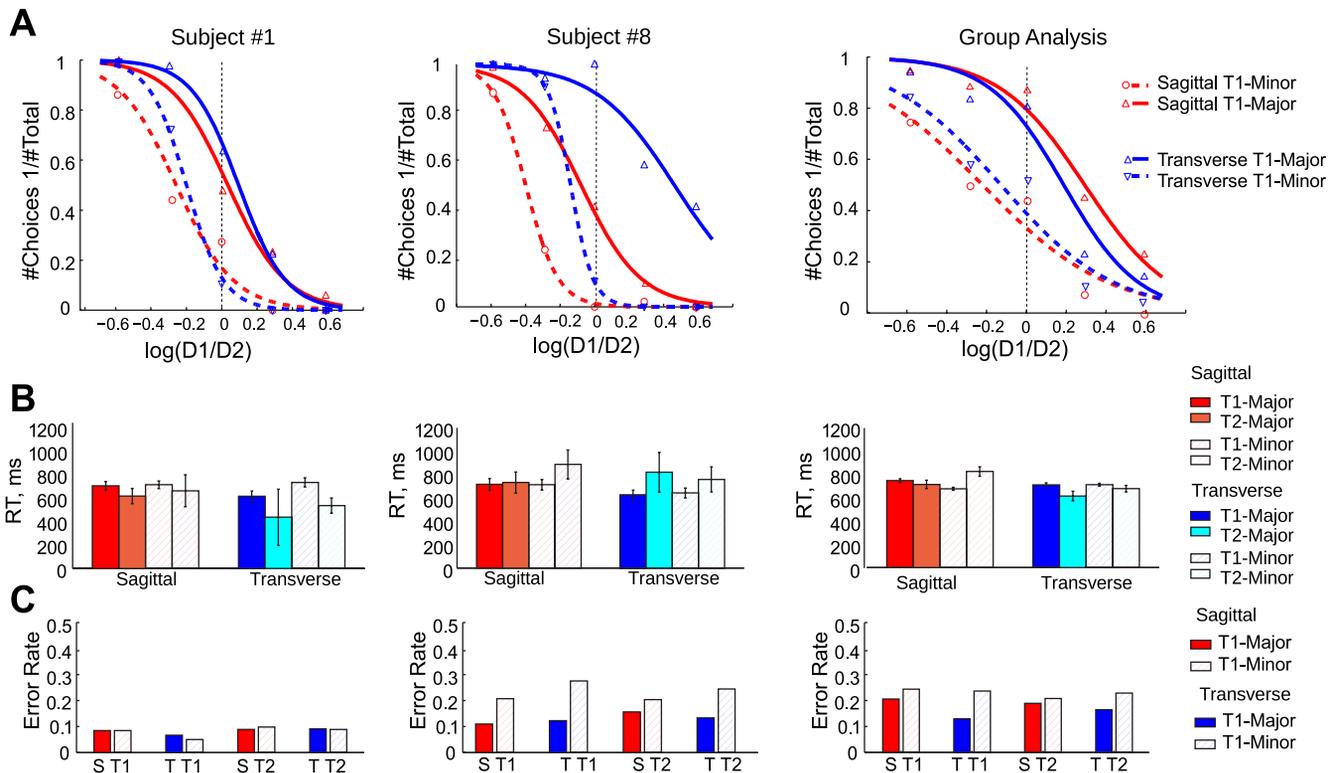
Fig. 3. Target preference curves, reaction times (RTs), and error rates for two subjects and for the complete group of subjects ($n = 12$). *A*: T1 preference curves. The sigmoids show the preference for T1 over the total number of correct choices for T1 major versus T1 minor cases as a function of relative target distance from the origin (D_1/D_2). For the two subjects shown as well as for the group analysis, T1 major curves were shifted to the right of the T1 minor curves, suggesting a strong effect of biomechanics. *B*: RTs (means ± SE) for the same two subjects and collapsed across all subjects for all four geometric arrangements. *C*: error rates for the same two subjects and collapsed across all subjects (proportion of errors over the total number of trials) in all four geometric environments.

tests showed nonsignificant differences in 8 of 12 subjects ($P > 0.05$; see Fig. 3*C*). Therefore, because error rates were similar across all movements, we conclude that they cannot strongly bias the choice.

Analyses of kinematics. Figure 4*A* shows typical trajectories from two-target trials in the four configurations shown in Fig. 2 for targets at equal relative distance (11 cm). The choices for all configurations showed that this subject preferred trajectories arriving along the major axis of the mobility ellipse. Figure 4*B* shows the tangential velocity profiles for one-target trials, aligned at the time that the stylus entered the via point. Although the profiles exhibited significant variability, the velocity tended to be smooth and single peaked. The movement was curved and the tangential velocity was not entirely symmetric, with the acceleration often longer than the deceleration (probably due to the requirement of sliding over the via point). This behavior was consistent across all directions. Although movement duration increased linearly with distance, it was not significantly different across directions.

Since the experimental setup was defined to maximize the differences at target arrival, we assessed end-point variability at the target along the direction of movement (on-axis scatter) and perpendicular to it (off-axis scatter) (Messier and Kalaska 1999). The off-axis scatter (aiming scatter) at target arrival was calculated as the minimal distance between the point at which the trajectory entered the target cue, and the average trajectory calculated after time alignment at target arrival. Comparisons between off-axis scatter distributions between T1 and T2 at each arrangement are shown in Fig. 5, *B* and *D* for a typical

subject. Although the overall effect was small, the average off-axis scatter tended to be smaller (narrower SD), if the trajectory was aligned with the major axis, for both the transverse and sagittal arrangements. We suggest that these differences are a consequence of the ease of aiming along the major axis of the mobility ellipse, but they are small because subjects can correct using continuous visual feedback. Major trajectories offer more resistance-potential perturbations perpendicular to the trajectory (off-axis). We calculated the off-axis endpoint distributions for each target and geometric arrangement (see Fig. 5, *B* and *D*) and found significant differences for the off-axis scatter ($P < 0.05$, K-S test) for 8 of 12 subjects. This was confirmed by multifactorial ANOVA with the following factors: major versus minor and sagittal versus transverse. Seven of twelve subjects exhibited significant sensitivity to major/minor and five of twelve subjects exhibited sensitivity to sagittal/transverse ($P < 0.05$). For the seven subjects reaching to targets that were defined by round cues (see MATERIALS AND METHODS), four of seven subjects were sensitive to major/minor and four of seven were sensitive to sagittal/transverse. As an interpretation of this trend, we suggest that these differences of end-point errors across conditions of different biomechanical cost are not the cause of the subjects' pattern of choice but rather a kinematic consequence of the differences in aiming ease resulting from the anisotropical distribution of biomechanics.

If off-axis scatter captures aiming precision in the direction perpendicular to movement, on-axis scatter captures variability along the direction of movement (stopping scatter), which
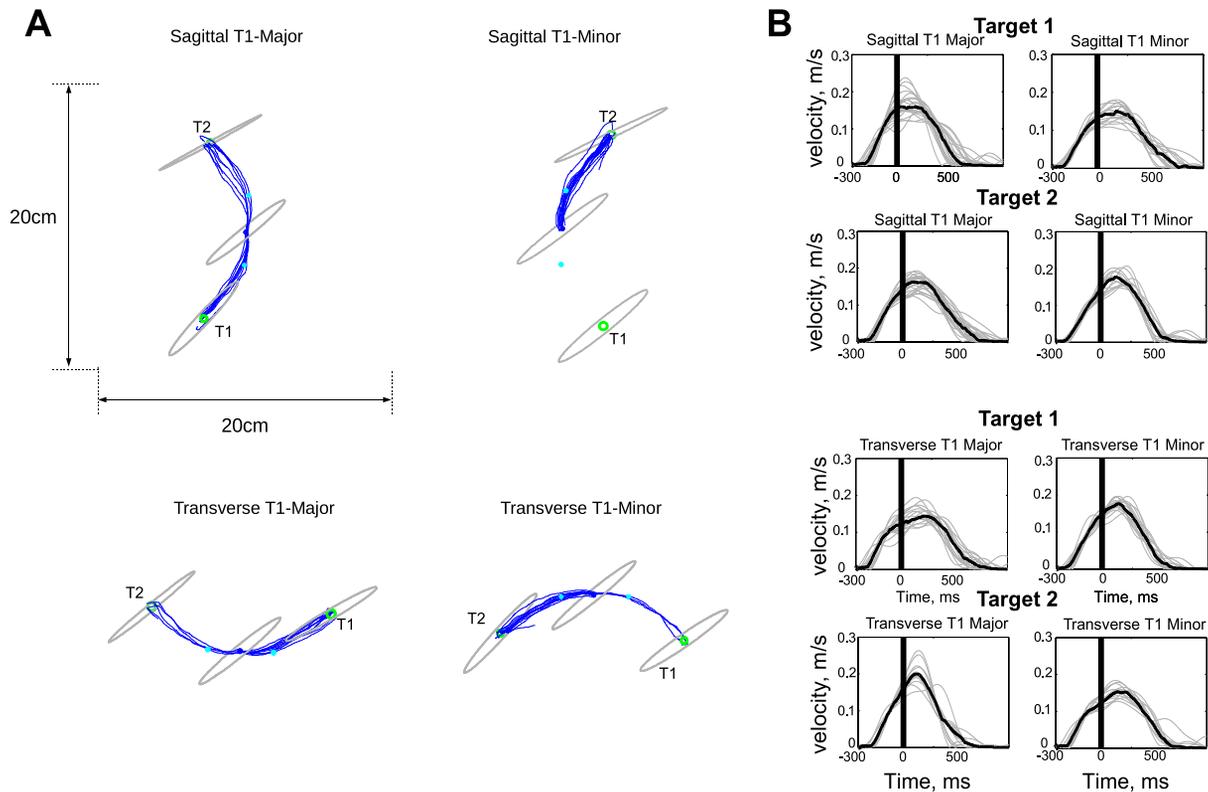
Fig. 4. Example kinematics. *A*: typical trajectories in each geometric arrangement for the case of equal distance to T1 and T2. T1 was chosen more often when the arrival trajectory was oriented along the major axis of the mobility/admittance ellipse. *B*: tangential velocities in one-target trials toward T1 and T2, aligned at the time of via point crossing in all four geometric arrangements. Velocities were, in general, bell shaped and single peaked in all cases.

reflects the difficulty of stopping the movement at the target. We calculated on-axis scatter at the target as the minimal distance between the stopping point and the axis perpendicular to the line defined by the center of the target cue and the average arrival vector. The resulting distributions for one typical subject are shown in Fig. 5, *B* and *D* for the transverse and sagittal arrangements. In general, the differences in on-axis scatter across conditions and targets were very small. For the five subjects performing the task with visible round targets, K-S tests among T1 major and minor trajectories revealed that only one subject exhibited significant differences ($P < 0.05$) between distributions. Among the seven subjects for whom the targets were not visible (their position was implied by acute triangles; see MATERIALS AND METHODS), four subjects exhibited significant differences for major/minor on-axis scatter distributions. This difference between subjects reaching toward visible versus nonvisible targets was significant, suggesting that arm control is facilitated when the target area is well defined. It is therefore not surprising that the effect of inertial anisotropies increased when the target regions were not explicitly shown. Accordingly, the on-axis scatter for trajectories arriving along directions of higher mobility/admittance tended to be slightly larger than along directions of lower mobility/admittance (larger inertia/stiffness). These results were reinforced by an additional multifactorial ANOVA with the following factors: major/minor and sagittal/transverse. In sessions with implied target regions, the on-axis scatter in four of seven subjects exhibited sensitivity to major/minor and in three of seven subjects exhibited sensitivity to sagittal/transverse. In contrast, when the target regions were explicitly shown, the

on-axis scatter exhibited sensitivity to major/minor in one of five subjects and to sagittal/transverse in two of five subjects. However, although this may suggest a trend, marginally consistent with the subjects' choices, we consider on-axis scatters as a kinematic consequence of the anisotropical distribution of biomechanics, and not the cause of subject choices.

Interaction torques. An additional factor that could potentially influence the selection of one target over another is interaction torques. To investigate this, we performed an analysis of the contribution of interaction torques to the shoulder and elbow joint torques for each possible movement in each arrangement (see *Interaction Torques* in MATERIALS AND METHODS). These are shown in Fig. 6 together with the average angular kinematics. For the case of the sagittal arrangements (Fig. 6, *top*), interaction torques (dashed lines) exerted a resistive contribution on the other segment (solid lines) (note that the solid and dashed lines exhibit the opposite sign at nearly all times during the trajectory) for both the shoulder and elbow. Therefore, we may conclude that at least for the sagittal arrangements, the contribution of interaction torques is not exerting a significant bias toward one target or another. The situation is more complicated for the transverse arrangements (see Fig. 6, *bottom*). For the transverse T1 major arrangement, interaction torques were mostly resistive for T2 and assistive for T1; for the transverse T1 minor arrangement, interaction torques were mostly assistive in both cases. Nevertheless, if interaction torques were a major factor influencing target preference, this should reflect a bias toward targets for which interaction torques assist or resist the movement consistently. However, this is not the case, as subjects consistently prefered
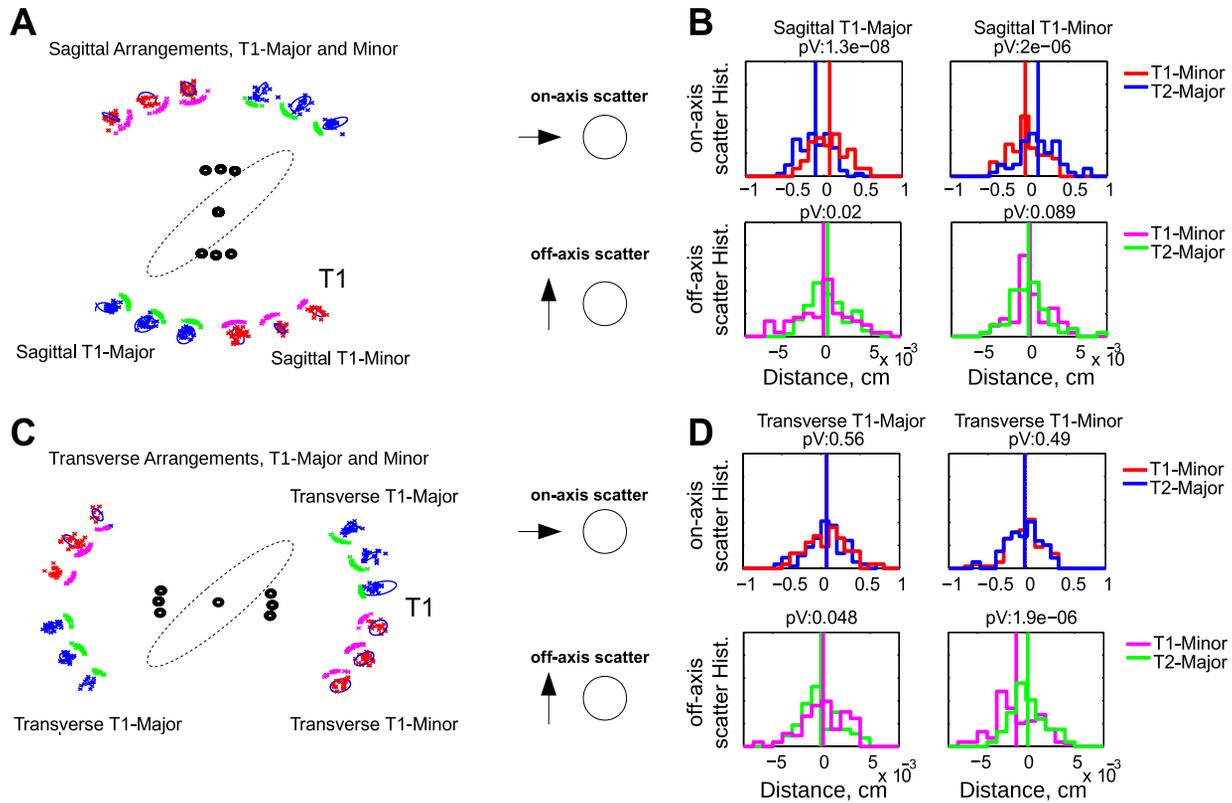
Fig. 5. Dispersion at the target for the case of equal distance to each target. *A*: positions at movement offset for the sagittal arrangements parametrized as a function of orientation and T1 stability. *B*: histograms of off-axis (aiming dispersion) and on-axis (extent) scatter for the sagittal T1 major and T1 minor arrangements. The *P* value (pV) shown at the *top* of each graph measures the similarity between both distributions shown in the picture [Kolmogorov-Smirnov (K-S) test]. *C*: positions at movement offset for the transverse arrangements parametrized as a function of orientation and T1 stability. *D*: histograms of off-axis and on-axis scatter for the transverse T1 major and T1 minor arrangements.

T1 for the T1 major arrangement and T2 for the T1 minor arrangement. Therefore, although interaction torques do influence motor planning and execution (Gribble and Ostry 1999), they are not likely to be responsible for the pattern of choices observed in the present study.

Energy considerations. Clearly, movements along the major axis of the mobility ellipse require less energy than movements along the minor axis, because the arm is more easily accelerated in the major direction. Our experiment does not perturb the arm or impose a force field and, therefore, does not dissociate energy from mobility/admittance. However, although we cannot establish which biomechanical factors may be responsible for subject choices, we designed the experimental setup to equalize the biome-
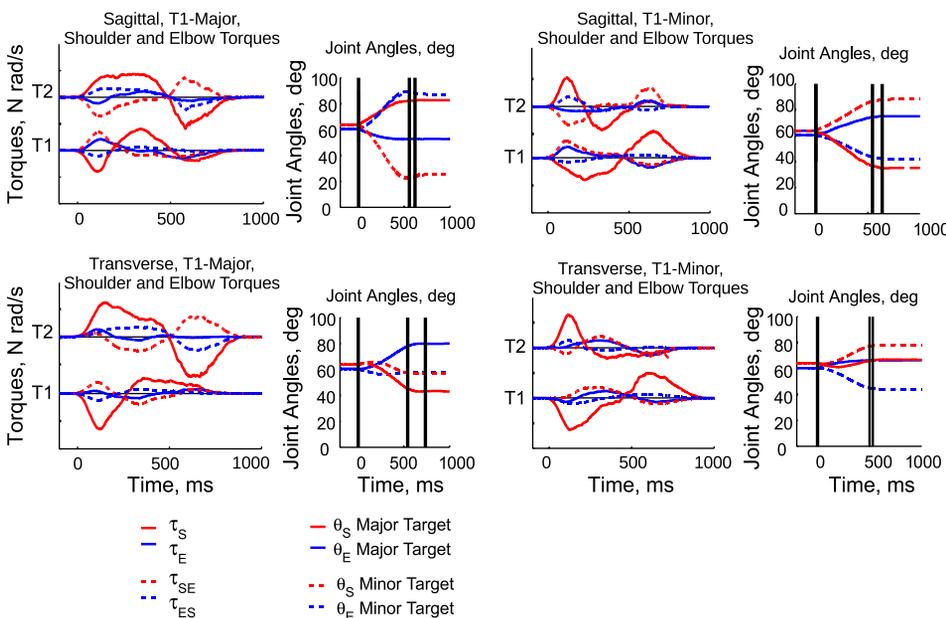

Fig. 6. Average torques and joint angles for reaching movements in all four geometric arrangements for the case of equal relative distance. The torque graphs display the net torques for the shoulder and elbow as solid red and blue lines, respectively, and their related interaction torques as dashed lines. Average joint angles for reaching movements toward either target are colour coded according to the joint (shoulder, red; elbow, blue) and the biomechanical case (major/minor). The vertical lines indicate the movement onset and the moment when the subject enters the target.

chanical cost at launching time and to maximize its difference at the target arrival.

To make sure that differences of the subject's target preference depend on the difference between the biomechanical costs at the end of the two movements, we needed to make sure that the force required to initiate both movements was approximately similar. To this end, we calculated and compared the energy required to initiate movement (the launching cost) in the directions toward either via point. Specifically, we calculated the muscle work necessary to reach from the origin to each via point within each arrangement by integrating the muscle torques (total joint torque minus interaction torques) between the origin and the via point for the chosen direction for each individual trial (see *Eq. 8*). The values obtained were used to estimate the distribution of launching cost and plotted separately for each of the four arrangements in Fig. 7. Each of the four subplots shows the histograms of launching muscle work for reaching toward T1 (red) and T2 (green). These distributions did not exhibit significant differences ($P > 0.05$, paired K-S test) for 10 of 12 subjects. This implies that the differences in target preference exhibited by most subjects must depend on factors other than launching cost. In other words, the decision cannot be simply determined by the ease of initiating either reaching movement (like sliding along a valley in an energy surface) but must take other factors, such as predicted biomechanics, into account. We will return to this point in the DISCUSSION.

Although this result indicates that the symmetry of the launching directions equalizes the energy costs of the launching phase of the two potential actions in addition to the launching mobility, the sequence of muscle activations to initiate each movement is certainly different (see Fig. 8). This difference may provide a different subjective perception of movements toward different targets and could therefore exert significant influence on choice preference. To clarify this issue, we performed additional control experiments using configurations in which both potential trajectories share the same via point and therefore involved initiating the movement with the same sets of muscles (see Supplemental Material). In this

control condition, four of four subjects exhibited a statistically significant preference for trajectories offering a major arrival. In other words, a similar preference for major arrival trajectories was observed even when the launching phase of the potential movements was identical.

Path curvature. One potential confound may also have been trajectory curvature, which may influence the complexity of execution (Torres and Andersen 2006). To analyze this, we calculated the curvature (K; see MATERIALS AND METHODS) of each trajectory and normalized it by path distance. The results show that K values were practically indistinguishable between the two potential movements, independently of geometric arrangement and distance (data not shown). Therefore, relative path curvature cannot be responsible for target preferences.

Target location versus arm biomechanics. One final potential confound we considered is that subject preferences may be related to the different spatial location of the targets rather than to the biomechanics of the arrival trajectory. In other words, it may be possible that a target is chosen more often because subjects prefer the region of space where the target is placed. To test this, we performed a control experiment (described in the Supplemental Material) in which the geometric arrangements were designed in such a way that the same target was sometimes approached from a major direction and other times from a minor direction. In general, we again found that subjects preferred targets that were approached along the major axis. This suggests that it is the biomechanics of arrival at the target, not its location in space, that has the major influence on choices.

DISCUSSION

Although a variety of studies have examined the cognitive factors involved in decision making (Glimcher 2002; Gold and Shadlen 2007; Kennerley et al. 2009), including risk (Kahneman and Tversky 1979), spatial discounting (Stevens et al. 2005), and reward (Miller et al. 2002; McClure et al. 2003), much less attention has been devoted to understanding if, how, and when biomechanical factors are involved in decisions.
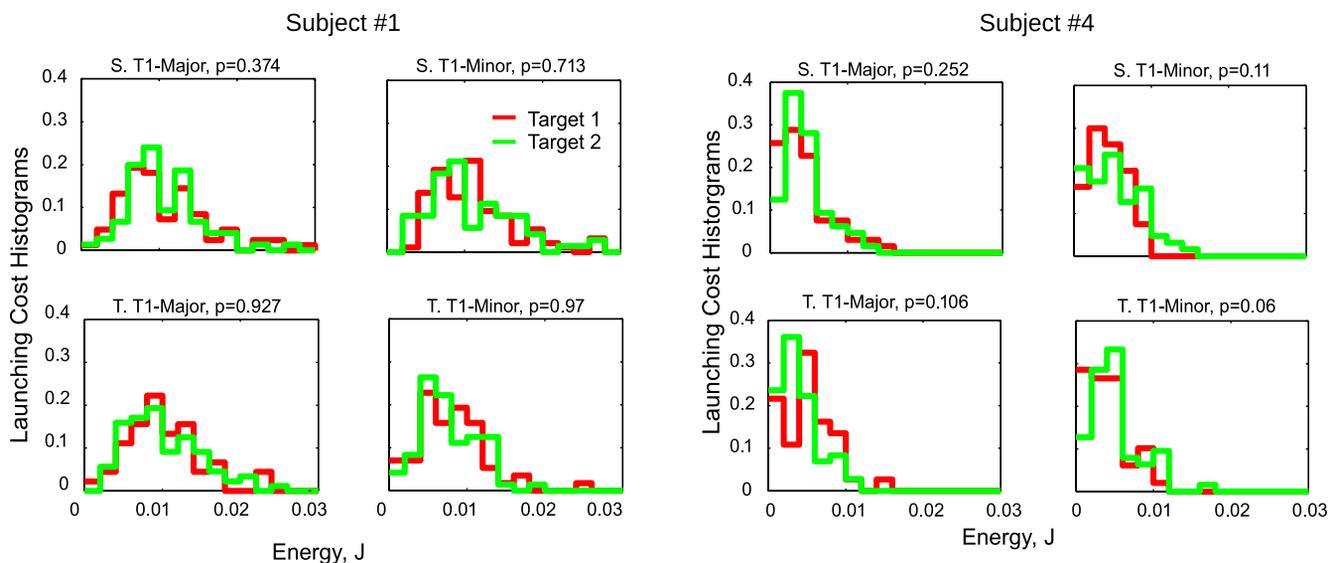

Fig. 7. Histograms of the launching cost (muscle work) for both potential trajectories in each geometric arrangement for *subjects 1* and *4*. The *P* values shown at the *top* indicate that the muscle work to reach *via point 1* or *via point 2* was similar ($P > 0.05$ in all cases, K-S test).
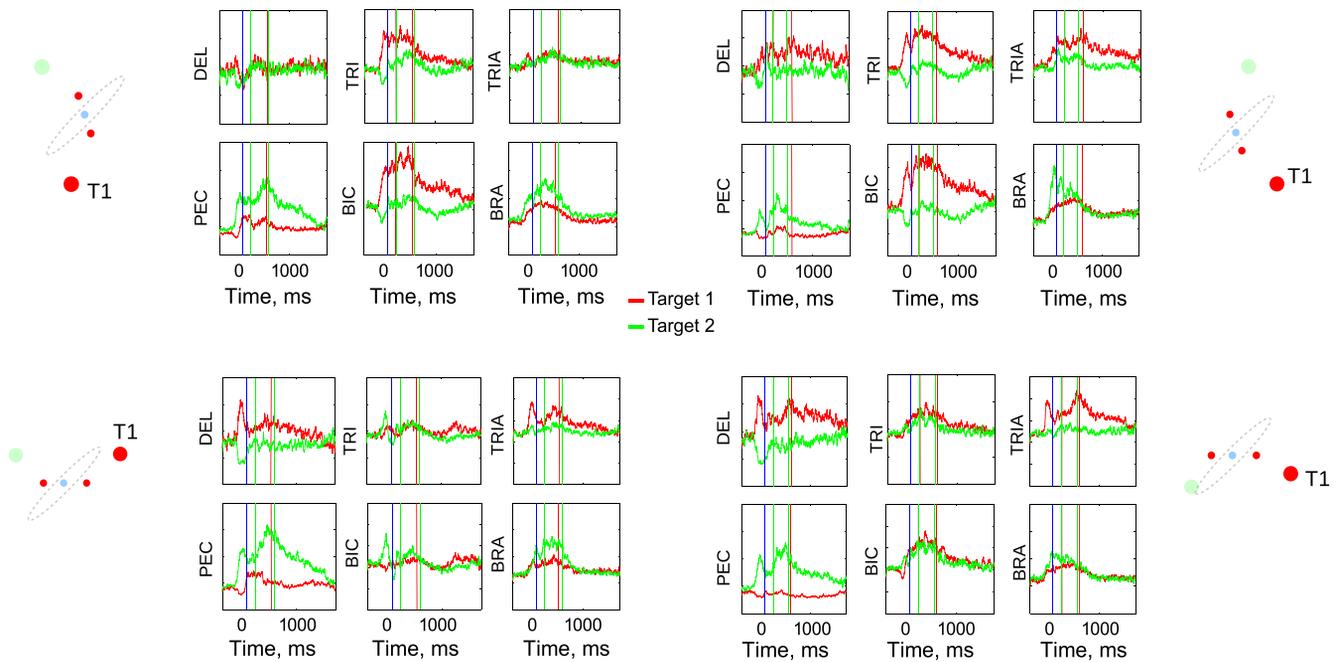
Fig. 8. Average muscle activity for reaching movements toward T1 (red) and T2 (green) in all four geometric arrangements. Activity for three extensors (*top*) and three flexors (*bottom*) is plotted. The three extensors are the posterior deltoid (DEL), triceps long head (TRIO), triceps lateral head (TRIA); the three flexors are the pectoralis major (PEC), biceps long head (BIC), and brachioradialis (BRA). The blue vertical line indicates the movement onset, and the subsequent red or green vertical lines indicate via point crossing and target acquisition, respectively.

However, given that different movements may achieve the same goal and that these movements differ in metabolic cost as well as stability properties, we should expect biomechanical factors to influence decisions involving a motor response. Furthermore, decisions involving motor responses, such as flight versus fight, turn right versus turn left, forage versus rest, have dominated animal behavior far longer than abstract decisions such as moving a knight or a bishop during a chess game. Consequently, we should expect that the mechanisms for action selection have been influenced by biomechanical factors long before they became capable of making the kinds of abstract decisions for which biomechanics would not matter.

The results shown above demonstrate that biomechanics is a factor that can influence selection of motor actions. Although this may not be the case in all experimental paradigms, we can certainly picture many natural situations in which the prediction of biomechanics may be necessary and advantageous 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 they are able to predict the biomechanics of 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 (Baumann et al. 2009; Cisek and Kalaska 2002, 2005; McPeek and Keller 2002), and it has been suggested that these representations compete for overt execution (Cisek 2007). As decision variables are computed and gradually fine tuned, they can bias the competition to favor the "better" choice. We suggest that this bias includes biomechanical information that is estimated before movement onset. There is significant neurophysiological evidence suggesting that the prediction of biomechanical factors may involve the cerebellum, which may contribute to action selection

through its projections to premotor and primary motor regions (Pasalar et al. 2006; Bastian 2006).

In our experiments, we examined how the biomechanics of potential movements influence choices between them by varying the relative path length and the biomechanical properties of the trajectory. Our results demonstrate that when humans are given a free choice between two actions that are equivalent from a visual perspective (relative path curvature, hemifield, etc.), biomechanical factors exert a significant influence on their choices. In particular, if the hand arrives at a given target along a trajectory aligned with the major axis of the mobility/admittance ellipse (T1 for T1 major and T2 for T1 minor), that target tends to be selected more frequently than the other, sometimes even when the target is further away. Furthermore, since the biomechanical differences between trajectories appear only later in the movement, subjects' preferences must be driven by a prediction of the biomechanics estimated before movement onset. Thus, our results not only demonstrate the role of biomechanics in decision making but also offer an affirmative answer to the question of whether the brain is capable of predicting biomechanics before movement onset.

Physical and anatomic factors involved. The notion of biomechanics can include a number of factors. Throughout this report, we used the alignment of the trajectory with the major/minor axes of the mobility/admittance ellipse as a measure of arm biomechanics. In a similar fashion, Sabes and Jordan (1997) used three metrics to assess the potential role of biomechanics in the planning and execution of trajectories around an obstacle: manipulability, mobility, and admittance. Manipulability relates joint motion to end-point uncertainty and is defined as $\mathbf{J}(\theta)\mathbf{J}(\theta)'$, where $\mathbf{J}$ is the Jacobian transforming joint angles into end-point space. Therefore, manipulability captures the anisotropies resulting from the morphology of the arm, which influences the transformation of noise from joint space

into end-point variability. Admittance (the inverse of mechanical stiffness) is defined as the ratio between displacement and force and thus depends on the viscoelastic properties of the arm. In other words, if the arm is perturbed by a small force and the arm's admittance is known, we can predict its resulting displacement. Finally, mobility is defined as the ratio between acceleration and force. In the same manner, if the arm's mobility is known, we can predict the arm's acceleration after a given perturbation. Therefore, whereas admittance captures the arm's active properties (viscoelastic state), mobility captures the anisotropies resulting from the morphology of the arm and its distribution of mass, i.e., its passive properties (see MATERIALS AND METHODS for further detail). Although Sabes and Jordan found that all of these three metrics covaried to a significant degree with the planning of the critical point of their obstacle avoidance trajectory, mobility was the one that gave the best fit.

Accordingly, we used the alignment of the trajectory at the target with the major/minor axis of the mobility ellipse as a metric of arm biomechanics. Although this characterization may disregard some of the subtleties that a complete musculoskeletal model of the arm would include, such as muscle placement, it does capture the anisotropies resulting from the arm's morphology and distribution of mass as well as its viscoelastic properties. Therefore, it is a reasonably accurate "first-order" metric to assess the influence of biomechanics on decision making.

Although our results demonstrate that biomechanics exert a significant influence on target preference and that these correlate with arm mobility and, therefore, to some extent with arm admittance, they do not specifically quantify the contribution that each potential biomechanical factor may have on influencing selection. In principle, the preference for major trajectories should improve aiming accuracy, as the hand moving along this direction would be least sensitive to potential perturbations perpendicular to the trajectory. However, easy aiming should be viewed as a consequence of the arm's biophysical properties along those directions. In other words, the fact that movements along the "major" directions in the geometric arrangements mostly involve the forearm is also consistent with movement along directions of maximal mobility/admittance (and, therefore, minimal inertia/stiffness). The results support this reasoning, suggesting that aiming along those directions should be easier.

In addition to this, the ease of stopping at the target after arrival is also dependent on arm biomechanics. Assuming that movements along all directions were made at comparable velocities (see Fig. 4*B*), one should expect on-axis accuracy to be worse in movements arriving along the major axis, which require an active braking force. Lametti and Ostry (2010) showed that end-point error varies as a function of stiffness. We did not observe such a result, possibly because our movements were considerably slower (peak velocity of 15–20 cm/s as opposed to 35 cm/s), giving subjects more time to compensate for variability using visual feedback.

Biomechanics and energy. Several studies have suggested that trajectory planning is influenced by metabolic energy costs (Alexander 1997; Guigon et al. 2007; Goble et al. 2007) and may therefore also influence target preferences in our experiment. However, we suggest that these preferences cannot only be due to difference in the cost of movement energy. Our analysis shows that the muscle work required for movements along the major axis of the mobility ellipse is lower than for those along its minor axis. Nevertheless, as shown by the

preference curves, subjects often select movements whose required energy is larger, meaning that additional factors, other than energy, are exerting a bias on the choice.

Our results raise the question of whether the biomechanical factors that influence decisions are computed de novo on each trial or whether they are already precomputed and simply recalled as subjects visually inspect the scene. Although there may be no practical behavioral difference between these possibilities, the question bears upon the existence or absence of a forward internal model that predicts biomechanics and on where such a model may reside in the brain. The cerebellum has often been implicated in the calculation of biomechanical factors in anticipation of movement onset (Uno et al. 1989; Bastian 2006), and it has been suggested that an internal model with some partial account of biomechanics is present (Pasalar et al. 2006). Our results demonstrate that at least some knowledge of biomechanics exists before movement onset, while the decision is being made, supporting the possibility that the same knowledge may be used to ultimately guide movement execution.

DISCLOSURES

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

REFERENCES

Alexander RM. A minimum energy cost hypothesis for human arm trajectories. *Biol Cybern* 76: 97–105, 1997.

Bastian AJ. Learning to predict the future: the cerebellum adapts feed-forward movement control. *Curr Opin Neurobiol* 16: 645–649, 2006.

Baumann MA, Fluet MC, Scherberger H. Context-specific grasp movement representation in the macaque anterior intraparietal area. *J Neurosci* 29: 6436–6448, 2009.

Churchland MM, Afshar A, Shenoy KV. A central source of movement variability. *Neuron* 52: 1085–1096, 2006.

Cisek P. Cortical mechanisms of action selection: the affordance competition hypothesis. *Philos Trans R Soc Lond B Biol Sci* 362: 1585–1599, 2007.

Cisek P, Kalaska JF. Neural mechanisms for interacting with a world full of action choices. *Annu Rev Neurosci* 33: 269–298, 2010.

Cisek P, Kalaska JF. Simultaneous encoding of multiple potential reach directions in dorsal premotor cortex. *J Neurophysiol* 87: 1149–1154, 2002.

Cisek P, Kalaska JF. Neural correlates of reaching decisions in dorsal premotor cortex: specification of multiple direction choices and final selection of action. *Neuron* 45: 801–814, 2005.

Efron B. *The Jackknife, the Bootstrap and Other Resampling Plans*. Philadelphia, PA: Cambridge Univ. Press, 1982.

Flash T. The control of hand equilibrium trajectories in multi-joint arm movements. *Biol Cybern* 57: 257–274, 1987.

Glimcher P. Decisions, decisions, decisions: choosing a biological science of choice. *Neuron* 36: 323–332, 2002.

Goble JA, Zhang Y, Shimansky Y, Sharma S, Dounskaia NV. Directional biases reveal utilization of arm's biomechanical properties for optimization of motor behavior. *J Neurophysiol* 98: 1240–1252, 2007.

Gold JI, Shadlen MN. The neural basis of decision making. *Annu Rev Neurosci* 30: 535–574, 2007.

Gordon J, Ghez C. Trajectory control in targeted force impulses. III. Compensatory adjustments for initial errors. *Exp Brain Res* 67: 253–269, 1987.

Gribble PL, Ostry DJ. Compensation for interaction torques during single- and multijoint limb movement. *J Neurophysiol* 82: 2310–2326, 1999.

Guigon E. Active control of bias for the control of posture and movement. *J Neurophysiol* 104: 1090–1102, 2010.

Guigon E, Baraduc P, Desmurget M. Computational motor control: redundancy and invariance. *J Neurophysiol* 97: 331–347, 2007.

Hogan N. Impedance control: an approach to manipulation: part I–theory. *J Dyn Sys Meas Control* 107: 1–7, 1985a.

Hogan N. Impedance control: an approach to manipulation: part II–implementation. *J Dyn Sys Meas Control* 107: 8–16, 1985b.

Hogan N. Impedance control: an approach to manipulation: part III–applications. *J Dyn Sys Meas Control* 107: 17–24, 1985c.

Hua SE, Houk JC. Cerebellar guidance of pre-motor network development and sensorimotor learning. *Learn Mem* 4: 63–76, 1997.

Kahneman D, Tversky A. Prospect theory: an analysis of decision under risk. *Econometrica* 47: 263–291, 1979.

Kaminski TR, Gentile AM. A kinematic comparison of single and multijoint pointing movements. *Exp Brain Res* 78: 547–556, 1989.

Kennerley SW, Dahmubed AF, Lara AH, Wallis JD. Neurons in the frontal lobe encode the value of multiple decision variables. *J Cogn Neurosci* 21: 1162–1178, 2009.

Lametti DR, Ostry DJ. Postural constraints on movement variability. *J Neurophysiol* 104: 1061–1067, 2010.

McClure SM, Daw ND, Montague PR. A computational substrate for incentive salience. *Trends Neurosci* 26: 423–428, 2003.

McPeek RM, Keller EL. Superior colliculus activity related to concurrent processing of saccade goals in a visual search task. *J Neurophysiol* 87: 1805–1815, 2002.

Messier J, Kalaska JF. Comparison of variability of initial kinematics and endpoints of reaching movements. *Exp Brain Res* 125–2:, 1999139–152.

Miller EK, Freedman DJ, Wallis JD. The prefrontal cortex: categories, concepts and cognition. *Philos Trans R Soc Lond B Biol Sci* 357: 1123–1136, 2002.

Morasso P. Spatial control of arm movements. *Exp Brain Res* 42: 223–227, 1981.

Pasalar S, Roitman AV, Durfee WK, Ebner TJ. Force field effects on cerebellar Purkinje cell discharge with implications for internal models. *Nat Neurosci* 9: 1404–1411, 2006.

Sabes PN, Jordan MI. Obstacle avoidance and a perturbation sensitivity model for motor planning. *J Neurosci* 17: 7119–7128, 1997.

Sabes PN, Jordan MI, Wolpert DM. The role of inertial sensitivity in motor planning. *J Neurosci* 18: 5948–5957, 1998.

Soechting J, Lacquaniti F. Invariant characteristics of a pointing movement in man. *J Neurosci* 1: 710–720, 1981.

Stevens JR, Rosati AG, Ross KR, Hauser MD. Will travel for food: spatial discounting in two new world monkeys. *Curr Biol* 15: 1855–1860, 2005.

Todorov E, Jordan MI. Optimal feedback control as a theory of motor coordination. *Nat Neurosci* 5: 1226–1235, 2002.

Torres E, Andersen R. Space-time separation during obstacle-avoidance learning in monkeys. *J Neurophysiol* 96: 2613–2632, 2006.

Uno Y, Kawato M, Suzuki R. Formation and control of optimal trajectory in human multijoint arm movement. *Biol Cybern* 61: 89–101, 1989.

Vindras P, Desmurget M, Viviani P. Error parsing in visuomotor pointing reveals independent processing of amplitude and direction. *J Neurophysiol* 94: 1212–1224, 2005.