Effort, success, and nonuse determine arm choice

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Schweighofer N. Xiao Y. Kim S. Yoshioka T. Gordon J. Osu R. Effort, success, and nonuse determine arm choice. J Neurophysiol. 114: 551–559, 2015. First published May 6, 2015; doi:10.1152/jn.00593.2014.—How do humans choose one arm or the other to reach single targets in front of the body? Current theories of reward-driven decisionmaking predict that choice results from a comparison of “action values,” which are the expected rewards for possible actions in a given state. In addition, current theories of motor control predict that in planning arm movements, humans minimize an expected motor cost that balances motor effort and endpoint accuracy. Here, we test the hypotheses that arm choice is determined by comparison of action values comprising expected effort and expected task success for each arm, as well as a handedness bias. Right-handed subjects, in either a large or small target condition, were first instructed to use each hand in turn to shoot through an array of targets and then to choose either hand to shoot through the same targets. Effort was estimated via inverse kinematics and dynamics. A mixed-effects logistic-regression analysis showed that, as predicted, both expected effort and expected success predicted choice, as did arm use in the preceding trial. Finally, individual parameter estimation showed that the handedness bias correlated with mean difference between right- and left-arm success, leading to overall lower use of the left arm. We discuss our results in light of arm nonuse in individuals’ poststroke.

motor control; reaching; decisionmaking; motor cost; motor effort

ALTHOUGH WE ARE SELDOM AWARE of it, we constantly make decisions to use one arm or the other to reach or pick up objects. We usually reach with the hand ipsilateral to the target, e.g., Bishop et al. (1996) and Bryden et al. (2000). Hand use is not symmetrical, however, with an overall greater use of the dominant hand for targets straight ahead of the body midline (Coelho et al. 2013; Han et al. 2013; Przybyla et al. 2013) and for more “complex tasks,” such as grasping (Calvert and Bishop 1998; Mamolo et al. 2006).

What are the mechanisms underlying such discrete arm choices? Human choice has often been explained in terms of values or expected rewards (Behrens et al. 2007; Gershman et al. 2009; O’Doherty et al. 2004; Schweighofer et al. 2008). In this framework, the difference in expected rewards between the two arms, defined, for example, as reaching success (Han et al. 2008), is used to model the probability of arm choice via a softmax function. In an arm-choice experiment, in which the rate of reaching success was manipulated, subjects shifted the angle of equiprobable right/left-arm choice in the direction of the comparatively less-rewarded arm (Stoloff et al. 2011). This change in arm choice was well accounted for by a difference between expected rewards, updated via reward-prediction errors (Sutton and Barto 1998). Unlike these “good-based” models, however, “action-based” models, in which the values depend both on expected rewards and action costs, offer a better alternative to explain action choice (Cisek 2012; Crosson et al. 2009). For instance, the biomechanical properties of the arm influence the planning of reaching movements to minimize collisions with obstacles (Sabes and Jordan 1997) or when subjects choose between two targets (Cos et al. 2011). These previous studies thus suggest that some form of expected, motor-related costs (or equivalently, negative rewards) influences discrete arm choices. In optimal control models, minimization of motor costs provides a principled way of selecting one of many possible reaching movements (Todorov and Jordan 2002). Costs are often taken as the weighted sum of a final position-error term and of an effort term, computed as the square of the motor commands, e.g., Todorov and Jordan (2002).

Here, we propose a novel model for arm choice that directly links the characteristics of movements to actual choice. We hypothesize that in a shooting task with low-accuracy requirements, arm choice for each target depends on the between-arm difference in expected motor effort and on an overall handedness bias. We hypothesized further that in a shooting task with higher accuracy requirements, choice additionally depends on the between-arm difference in expected task success. To test these hypotheses, we performed an experiment in which right-handed subjects were first forced to use each hand in turn to shoot quickly through an array of targets, either in a large target condition, yielding a high success rate, or in a small target condition, yielding a lower success rate. Then, subjects chose whichever hand to shoot through the same targets. Action values were computed as the weighted sum of expected effort and expected success, which was estimated in forced trials. By rewriting the softmax choice model as a logistic-regression model, we directly estimated the relative effect of expected effort and success on choice, with the regression-constant parameter accounting for overall bias in left/right-arm choice.

METHODS

Subjects and Experimental Conditions

Twenty-six right-handed subjects (age 23.5 ± 1.9 SD; seven women), with no declared neurological impairments, participated in this study. The experiment was undertaken with the understanding and
written consent of each subject. The study conforms to the World Medical Association Declaration of Helsinki and was approved by the Advanced Telecommunications Research Institute Ethics Committee. Because success rate influences arm choice (Stoloff et al. 2011), subjects participated in one of two conditions, determined by target size. In the large target condition, a 3-cm target diameter was chosen to allow for high success rates with both arms for all targets. In the small target condition, a 2-cm target diameter reduced task success. Fourteen subjects participated in the first condition; the other 12 in the second conditions. All subjects were tested to be right handed with the Edinburgh Handedness Inventory (results of test: laterality quotient $0.85 \pm 0.17$ SD). One subject was right handed with correction (he used to be left handed but was instructed to be right handed). We excluded any subjects who used either hand $<5\%$ of the time in the free trials. As a result, the data from two subjects in the first condition were excluded, because these subjects used only their left hands four and five times out of 192 free-choice movements, respectively.

**Experimental Setup**

Subjects, who were sitting in a dental chair with a belt to minimize trunk movements, were instructed to move one arm quickly and accurately and shoot through a target using a bimanual robotic manipulandum that allowed horizontal movements with either hand. Twenty-four targets were equally spaced in the four quadrants every $15^\circ$ on a circle of 10 cm in radius from the home position (see Fig. 1). The target diameter depended on the experimental condition (see above for details). The home position was 3 cm in diameter. Shoulder and elbow angles at the starting home position were set at $40^\circ$ and $90^\circ$, respectively, for each subject based on the measurement of forearm and upper-arm length, as shown in Fig. 1. As in Stoloff et al. (2011) and Coelho et al. (2013), the two cursor positions, representing the hand positions (blue for right; red for left), were shifted horizontally, such that the hands visually appeared on the same home position when at the resting positions (see Fig. 1). Vision of the arm and hands was blocked at all times by a horizontal board mounted above the manipulandum on which the target and cursors were projected.

**Forced and Choice Trials in the Two Conditions**

For each condition, the experiment comprised eight trial blocks. For each trial block, one target was pseudorandomly selected from the set of 24 targets. A trial block consisted of three fast, outward-shooting movements: two forced movements, one for each arm, and one free-choice movement. One of the cursors first lit up to instruct the subject to use either the right or the left arm to shoot through the target. Appearance of the target served as a “go” signal (red for left; blue for right). After the subject’s shooting movement toward the target (forced movement 1), the robot returned the subject’s hand to the home position, and the other cursor lit up to instruct the subject to use the other arm to shoot through the same target (forced movement 2). The instructions to move either the right or left arm in the two forced movements were pseudorandomly drawn and counterbalanced across trials. During these forced movements, the other arm was prevented from moving by setting a large stiffness on its robotic arm. Finally, after the robot again returned the subject’s hand to the home position, both cursors lit up, the target turned white, and the subject was instructed to use either arm to reach the target (free-choice movement).

Overshoot was allowed, and stopping at the target was not required. A trial was successful if the cursor hit the target 270 ms or less after it left the home position in the large target condition and 300 ms or less in the small target condition. (This 30-ms difference in maximum movement duration was determined after piloting to take into account the shorter distance needed for success in the large target condition.) To show success, the home-position target disk became solid white if the cursor entered the target area within the allocated time. For unsuccessful trials, the home-position disk remained dark, and a beep sound was provided. The robot then returned the subject’s hand to the home position. The cursor corresponding to the moving hand was not visible during the movement after it left the home position. However, in a familiarization session before the experiment, the subjects first practiced reaching to the targets in the same way as in the actual experiment but with full cursor vision (48 trial blocks).

Movement data were filtered (5 Hz, Butterworth filter) for further analysis. In the analyses, we detected and excluded invalid trials, for which the minimal distance between the hand trajectory and the target center was $>5$ cm. According to this criterion, $<2\%$ of trials were excluded from the analyses. Note that use of the robots provided three advantages in our experiment: first, we could record position data at 200 Hz and thus derive a good estimate of accelerations to estimate effort; second, we could block the other arm in the forced movements to prevent additional invalid trials; third, the robots returned the subject’s hand to the home position after the hand position stabilized.

**Movement Success Data Analysis**

Task success in the forced conditions at each trial was recorded when the shortest distance between the target center and the hand path was less than the target radius. To analyze the success data for each arm in each condition, we performed mixed-effects logistic regression on success rates, with arm and condition as fixed factors and subjects as a random factor. (Note that we analyzed success rate and not binary success at each trial, because we used success rate in the predictive choice model below.) Differences between success rates in the left and right arm for each target were detected with pair-wise contrasts with sequential Bonferroni corrections for multiple comparisons. In the polar coordinate plots for success in Fig. 2, blue stars indicate that the success rate for the right arm is significantly greater than for the left arm; red stars indicate the opposite.

**Movement Effort Estimation Analysis**

We estimated the effort required to shoot through each target for each arm by simulating the experimental setup shown in Fig. 1 with two planar 2DOF arms. For each arm, hand position $(x, y)$, relative to the shoulder, was used to compute the elbow and shoulder angles $q = (q_2, q_3)$ using inverse kinematics. Then, the shoulder and elbow torques $\tau = (\tau_1, \tau_2)$ were estimated using inverse dynamics of a two-link manipulator. The torques were then used to compute the linear muscle commands at the shoulder and elbow joints (van Beers...
et al. 2004) via the following: \( u_i = T_e T_a \hat{\tau}_i + (T_e - T_a) \hat{\tau}_i + \tau_e \), where \( T_e \) and \( T_a \) represent excitation and activation time constants, respectively. All arm parameters were taken from van Beers et al. (2004). The commands were then squared [as usually done in optimal control models using effort; see, for instance, Todorov and Jordan (2002)] and then summed along the trajectory to compute total movement effort.

Specifically, effort was computed between the start of the movement, as defined by tangential velocity >5% of the maximum velocity, and the farthest position of the hand from the home target in the outward shooting movement. Mean effort was computed using the eight trials to each target with each arm in the forced condition.

**Arm Choice: Data Analysis**

For each target in the free-choice movements, we recorded right-arm choice over the eight free-choice trials. To analyze the binary right-arm choice data in each condition for each target, we first performed mixed-effects logistic regression, with condition and target location as fixed factors and subject as a random factor. To study whether right-arm choice at each target location was greater than the mean choice in each condition, we performed subsequent analyses with separate logistic-regression models with deviation contrasts for each condition. In the polar coordinate plots showing right-arm choice (Fig. 2), significant deviations from the mean right-arm choice are shown with symbol + or − near the targets.

**Arm Choice: Theoretical Model**

We made the following hypotheses to develop a theoretical rationale for the choice model. First, for each target, the arm with the highest action value, which is the expected reward given for this arm to reach the target, is preferred. Thus the probability of choosing the right arm for target \( k \) is modeled with a softmax function (which reduces to a sigmoidal function for two possible actions), as in reinforcement-learning models (Sutton and Barto 1998)

\[
P_{k,\text{right}} = \frac{1}{1 + e^{-\beta(V_{k,\text{right}} - V_{k,\text{left}})}}
\]

where \( V_{k,\text{right}} \) is the action value of using the right arm for movement to target \( k \), and \( V_{k,\text{left}} \) the action value of using the left arm; \( \beta \) is the decision model “inverse temperature.” According to this choice model, if \( V_{k,\text{right}} \) is high, then the exponential terms become small, and \( P_{k,\text{right}} \) approaches 1. The probability of choosing the left arm is simply

\[
P_{k,\text{left}} = 1 - P_{k,\text{right}}
\]

Second, for each target, the action values are given by the weighted sum of the difference in expected reward, that is, the difference in expected task success and the difference in expected effort (a negative reward) for each arm. In addition, a target- and movement-independent constant term provides an overall handedness bias. We thus rewrite Eq. 1 as

\[
P_{k,\text{right}} = \frac{1}{1 + e^{-\alpha(Success_{k,\text{right}} - Success_{k,\text{left}}) + \beta(Effort_{k,\text{right}} - Effort_{k,\text{left}}) + c}}
\]

where \( a, b, \) and \( c \) are parameters to be estimated, and the brackets \(< >\) indicate expected values of success and effort for the movement to target \( k \) based on previous movements to this target. In this equation, the intercept parameter \( c \) can be interpreted as a handedness bias, because if it is different from 0, it will bias choice to all targets.

**Arm Choice: Mixed-Effects Logistic-Regression Model**

To test the theoretical model above and estimate the model parameters, we performed mixed-effects logistic-regression analyses to predict choice. For this, we assumed that expected success and
expected effort for each arm are time invariant for the duration of the experiment. This would happen if subjects have learned these quantities either before the experiment or during the familiarization session. This assumption allowed us to use average success and effort for each arm and each target in the forced trials to predict individual choice in the free-choice trials. Specifically, with the use of right-left differences in mean effort and in mean success in the eight forced trials for each target as predictors, we predicted mean arm choice in the free-choice trials, as in Eq. 3. In addition, because reward-independent switching or perseverance is often seen in choice data, e.g., Lau and Glimcher (2005) and Rosenbaum et al. (1992), we added a term reflecting the history of previous movement in the forced condition. Specifically, we added a binary variable, taking the value one if the same hand was used in the immediately preceding forced-choice movement and zero otherwise.

A mixed-effects logistic-regression model, including the difference in expected effort and difference in expected success variables, is identical to the softmax function in Eq. 3, with the difference that the intercept is a now random effect; i.e., each subject has his or her own intercept, e, where i is subject. We developed and selected possible choice models using a forward-selection approach. We started with the simplest (base) model with random intercepts and then tested, in turn, the effect of the factor coding for the small/large target condition, the difference in expected effort, the difference in expected success, and the factor coding for prior history. We then tested a model that included the three terms—condition, effort, and success—and next tested models with all interactions among condition, effort, and success. We finally added the prior history factor to form the final (full) model. To improve convergence, both difference in expected success and expected effort were z transformed before being included in the model. Model fits were performed in R using the glmer function. Individual random intercepts were obtained with the function ranef. We compared the models using the Akaike Information Criterion (AIC) to account for different numbers of parameters, as AIC = −2 × LL + 2 × n, where n is the number of model parameter, and LL is the model log-likelihood. We tested for significance of additional terms in nested models via the Likelihood Ratio Test (LRT) using the R ANOVA function, which following glmer, allows for simple, yet systematic, comparisons of nested, logistic mixed models.

We also tested a model in which the difference in expected effort was replaced by expected right-hand effort only. Mental imagery studies show that timing similarities between actual and mental arm movements are accurate for all movement directions with the right arm but less so with the left arm (Gandrey et al. 2013). Therefore, it is possible that in advance of the choice, prediction of effort with the left arm is less accurate than with the right arm, and as a result, subjects only use the estimate of right-hand effort compared with an overall baseline before making a decision.

Finally, to check whether individual subjects were choosing their arm as a function of expected differences in effort, success, or both, we performed individual-subject logistic regressions for all subjects. In this analysis, we estimated fits using the pseudo McFadden’s R-square: \( R^2 = 1 - \frac{LL}{LL0} \), where LL is the log-likelihood, and LL0 is the log-likelihood of the null model (with intercept only).

RESULTS

Arm Choice

The comparison of the choice data for the right hand in the large and small target conditions (Fig. 2, A and B) demonstrates the following characteristics. First, the right hand is chosen more often than the left overall (mixed-effects logistic-regression model, \( P < 0.0001 \)). Second, the right hand is chosen more often in the small target condition (mixed-effects logistic-regression model, \( P < 0.0001 \)). In the large target condition, the mean of total right-hand use over all subjects is \( 68.4 \pm 2.8\% \) SE. In the small target condition, the mean of total right-hand use over all subjects is \( 77.7 \pm 4.2\% \) SE. Third, there is an effect of target location (mixed-effects logistic-regression model, \( P < 0.0001 \)), with right-arm choice appearing more pronounced in the upper-right and lower-left quadrants and is approximately distributed along an ellipse, with the mean long axis oriented at \( 40.3^\circ \) and \( 38.7^\circ \) for the large and small target conditions, respectively. The details of the target-location effect are shown in subsequent analyses, with separate logistic-regression models and deviation contrasts for each condition. In the large target condition, right-arm choices are greater than the mean for four targets in the first quadrant and for four targets in the third quadrant (deviation contrasts, \( P < 0.05 \); see Fig. 2A) and smaller than the mean for five targets in the second quadrant and four targets in the fourth quadrant. In the small target condition, choices are greater than the mean for four targets in the third quadrant and smaller than the mean for two targets in the second quadrant and for four targets in the fourth quadrant (deviation contrasts, \( P < 0.05 \); see Fig. 2B).

Task Success and Motor Cost

Task success. As expected, the reduction of target size from 3 cm in the large target condition to 2 cm in the small target condition reduced success rate (compare middle panels in Fig. 2, A and B; mixed-effects logistic-regression analysis, \( P < 0.0001 \)). In addition, success rate was lower for the left arm than for the right arm in both conditions (mixed-effects logistic-regression analysis, \( P < 0.0001 \)). Success rates in the large target condition are indicated: right arm, \( 87 \pm 2\% \); left arm, \( 83 \pm 2\% \); success rates in the small target condition are indicated: right arm, \( 79 \pm 5\% \); success left arm, \( 62 \pm 4\% \). Pair-wise, target-by-target comparisons show that success rates are generally higher with the right arm for movements to leftward targets than for movements to the same targets with the left arm. However, for most other targets, there is no advantage of either arm (\( P < 0.05 \) for all comparisons, Holm-Bonferroni corrections).

Motor cost. Effort varies for each target for the left and right arm but is qualitatively similar for the small and large target conditions, which was expected, because the allowed movement durations for the two conditions are similar (see METHODS). Because the inertia of the human arm at the hand forms an elongated ellipse with the main axis along the axis of the forearm (Gordon et al. 1994), the estimated effort is large for movements along this axis (see effort for movements to targets \( \sim 135^\circ \) and \( 315^\circ \) for the right arm and \( 45^\circ \) and \( 235^\circ \) for the left arm; see Fig. 2). Thus effort is much larger for the right arm in the second and fourth quadrants than for the left arm and vice versa for the left arm. These results suggest that effort plays an important role in choice; this possibility is tested more rigorously below. In addition, effort is comparatively greater for movements to targets away from the body than for targets toward the body (right arm: cost for target at 150° \( > \) cost for target at 330°, both target conditions, \( P < 10^{-4} \); left arm: cost for target at 30° \( > \) cost for target at 210°, both target conditions, \( P < 0.10^{-4} \)). Maximum acceleration at the hand was not different for movements in opposite quadrants for either arm (\( P > 0.05 \); thus effort for movements toward the body is smaller, because as the movement unfolds, extending the elbow increases the arm’s inertia compared with flexing the elbow.
Predicting Arm Choice: Effects of Effort, Success, Prior History, and Handedness Bias

Results from the mixed-effects logistic-regression analysis are summarized in Table 1. Figure 3 compares mean right-arm choice with predicted right-arm choice for large and small target conditions for three models: results from the model, including difference in expected effort and condition [model (2) in Table 1]; results from the model, including difference in expected success and condition [model (3) in Table 1]; and results from the model, including all significant terms [expected effort, expected success, condition, expected effort \times condition, and prior history; model (10) in Table 1]. As a reminder, both differences in expected effort and in success were z transformed before inclusion in the models. Although the addition of both expected effort and expected success significantly improves fit compared with model (1) with condition only (LRT \( P < 0.0001 \)), the addition of expected effort largely increases fit (AIC = 4,667) compared with expected success (AIC = 4,805), as can be seen by comparisons in Fig. 3. In addition, prior history of arm use on the preceding force-choice trial was a predictor of choice [model (4) in Table 1; comparison with model (1); LRT \( P < 0.0001 \)]. We tested for

### Table 1. Results of mixed logistic-regression model

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<tbody>
<tr>
<td>Effort</td>
<td>0.619* (0.041)</td>
<td>0.758* (0.060)</td>
<td>-0.655* (0.042)</td>
<td>-0.659* (0.043)</td>
<td>-0.673* (0.042)</td>
<td>-0.786* (0.061)</td>
<td>-0.675* (0.071)</td>
<td>-0.462* (0.041)</td>
<td>0.453* (0.042)</td>
<td>0.467* (0.041)</td>
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<tr>
<td>Success</td>
<td>0.391* (0.039)</td>
<td>0.417* (0.071)</td>
<td>0.417* (0.071)</td>
<td>0.462* (0.041)</td>
<td>0.467* (0.041)</td>
<td>0.466* (0.075)</td>
<td>0.417* (0.071)</td>
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<td>0.467* (0.041)</td>
<td>0.466* (0.075)</td>
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<tr>
<td>History</td>
<td>0.647+ (0.291)</td>
<td>0.730+ (0.329)</td>
<td>0.611+ (0.273)</td>
<td>0.651+ (0.293)</td>
<td>0.622+ (0.273)</td>
<td>0.671+ (0.303)</td>
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<td>0.677+ (0.303)</td>
<td>0.661+ (0.301)</td>
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<tr>
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<td>0.611+ (0.273)</td>
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<td>0.047 (0.047)</td>
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<td>Constant</td>
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<td>4.503</td>
<td>4.503</td>
<td>4.503</td>
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<td>AIC</td>
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AIC, Akaike Information Criterion; BIC, Bayesian Information Criterion; *P < 0.0001; †P < 0.001.
METHODS, this bias can be seen as a handedness normally distributed variable around the mean intercept. As expected, Fig. 4 shows a near-linear relationship between logit of effort and success for the small target conditions. Therefore, choice probability for each condition, with a differential effect on choice in the small target condition than in the large target condition.

Our final model (10) assumes that both effort cost and success rate have a linear influence on the logit of the arm-choice probability for each condition, with a differential effect of effort for the large and small target conditions. Therefore, we plotted the logit of the arm-choice probability as a function of effort for the large and small target conditions. The signs of the model parameters show that the probability of right-arm choice in free-choice trials is increased by the following: small targets, lower expected effort for the right arm than for the left arm, and prior history of right-arm use in the previous forced trial. Note that because the effort parameter is negative (it is a “cost”), the positive parameter for condition × expected effort shows that predicted effort has less of an effect on choice in the small target condition than in the large target condition.

We then tested a model in which only mean cost of the right arm was entered in the model, the target-independent cost for the left arm being included in the regression constant. This model did not fit the data as well as the model with the difference in effort (AIC = 4,536 vs. AIC = 4,486; LRT $P < 0.0001$), suggesting that comparison of the predicted effort for both arms occurs before the decision to use one arm or the other.

Logistic models were then fitted to each subject individually: we considered the two-parameter model with effort and bias (Model 1), the two-parameter model with success and bias (Model 2), and the three-parameter model with effort, success, and bias (Model 3). Results are reported in Table 2, which gives AIC, pseudo $R^2$, and the model selected according to smallest AIC for significant models for both conditions when the model fit was significant (using $\chi^2$ tests). For the large condition, individual model fits with the three-parameter model were relatively good, with $R^2 = 0.38 \pm 0.08$. Five out of 12 subjects’ arm choice were best fit by models including effort, two subjects with models including effort and success, and three subjects with models that included only success. The choice data for two subjects were not fit by any models. The behavior of these subjects departed radically from effort- and success-based predictions and from each other: one subject used almost exclusively his left arm for the left workspace, and another subject used almost exclusively his right arm for the left workspace. Overall model fits in the small target condition were similar to the large condition, with $R^2 = 0.40 \pm 0.06$, with all models significant. Five out 12 subjects’ arm choice were best fit by models including effort, five subjects with models including effort and success, and two subjects with models that included only success.

In the mixed logistic-regression model, the intercept is a normally distributed variable around the mean intercept. As discussed in METHODS, this bias can be seen as a handedness bias; a positive intercept will increase right-arm use over all targets. In Fig. 5, we show that the random intercept correlates with difference between mean-right and -left expected success for each subject ($r = 0.582$, $P < 0.0028$). Thus overall, subjects with increased success for the right arm compared with the left arm tend to exhibit greater use of the right arm than the left arm, regardless of effort and target location.
DISCUSSION

In this study, we drew from previous models of discrete choice based on action value and proposed that the probability of arm choice can be modeled as a softmax function of the between-arm differences in action values or equivalently, in expected cost. In addition, we drew from optimal control theory and proposed that the expected cost for each arm is composed of the weighted sum of motor effort and task success, which depend on final position error. By rewriting the softmax choice model as a logistic-regression model, we showed that arm choice in fast-shooting movements depends on the difference in expected effort between the right and left arm. Effort explains not only the greater ipsilateral hand use in the first and second quadrants but also the increase in left-arm use in the fourth quadrant compared with the first quadrant and the increase of right-arm use in the third quadrant compared with the second quadrant.

These results are consistent with previous studies showing that the central nervous system takes into account the biomechanical properties of the arm in decision tasks involving the arms. First, inertial properties of the arm appear to be used in planning reaching movements to minimize collisions with obstacles (Sabes and Jordan 1997). Similarly, when subjects are asked to choose between two targets, the biomechanical properties of the arm influence choice (Cos et al. 2011), with the preferred movements being those with final trajectories aligned along the small axis of the arm’s inertia at the hand. Results from these two previous studies and from the current study are thus compatible with data showing that pointing movements are modulated by the inertial anisotropy at the hand, with slower movements in directions of the larger inertia (Gordon et al. 1994). When selecting a posture at the end of the movement, subjects use predictions of kinematic variables in advance of the decision (Elsinger and Rosenbaum 2003). When instructed to produce reaching movements equally in all directions, subjects exhibit consistent biases in preferred directions, which can be accounted for by minimizing the effort needed to control intersegmental limb dynamics (Doumskata et al. 2011). A recent study showed that “change of mind” to reach a second target, as the movement was initially planned to a first target, is sensitive to energetic costs associated with the movement required to reach the second target (Burk et al. 2014). Finally, two other recent studies on arm choice suggest that biomechanical factors influence arm choice. Habagishi et al. (2010) showed that arm choice was affected by a force field applied on one hand via a robotic exoskeleton. Coelho et al. (2013) showed that the greater number of right (dominant)-arm choices for targets aligned on the body midline (and thus equidistant for each hand) corresponded to asymmetry in movement kinematics and dynamics, with the right hand more accurate and more efficient in using interaction torques to complete the reach.

Although our choice results are in line with those of Coelho et al. (2013) for the two midline targets, we found an increase of left-hand use in the fourth quadrant, whereas this previous study did not. Besides the use of robotic manipulanda vs. air sleds, there are three main differences between our experiment and that of Coelho et al. (2013). First, there was no vision of the cursor in our experiment, whereas there was full visual feedback in Coelho et al. (2013). This difference in visual feedback may be responsible for differences in arm choice (Przybyla et al. 2013). Second, subjects performed shooting movements in our experiment vs. reaching movements in Coelho et al. (2013). In our experiment, the mean velocity for all subjects was between 0.4 and 0.6 m/s, whereas in Coelho et al. (2013), the movements were rewarded if maximum hand velocity was >0.8 m/s. In our model, such high speed would increase the difference in effort between the two arms, which would predict even larger use of the left arm in the fourth quadrant. Although this is out of the scope of our analysis and model, we suggest that movement variability under high-speed conditions may explain, at least in part, the difference between the two studies. Because of the high speed in the Coelho et al. (2013) experiment, the greater signal-dependent noise in the motor command will lead to greater end-point variability than for the slower movements in our study. Our results show that with lower expected success, subjects chose to bias their hand use toward the dominant hand for all targets. An increased bias...
in the Coelho et al. (2013) study may account for at least part of the difference between the two studies. Finally, the initial arm posture was largely different in both studies. In our experiment, arm posture was the same for all subjects (shoulder and elbow angles at the starting home position were set at 40° and 90°, respectively), with a distance between arms of 0.36 ± 0.01 m. In contrast, in Coelho et al. (2013), the hands were separated by 0.60 m for all subjects, making the forearms near perpendicular to the torso. Such posture presumably leads to a large proprioception and vision mismatch. In addition, although this is speculative, it may be that reaching movements on each side of the body are strongly biased by laterality and may thus lead to results that are different from those in our study.

Arm choice in our study depends on the difference in motor cost, consisting of the weighted sum of expected effort and expected success, which in turn, depends on the error between the trajectory and the target. This cost is highly related to the costs used in optimal control models for movement control, e.g., Todorov and Jordan (2002). Our results thus suggest that motor costs that are used in the control of movement are also used in the discrete choice before movement execution. Optimal control models generate a number of desirable reaching-movement characteristics, such as bell-shape velocity profiles and increase of movement times in the directions of the highest effort, which correspond to the directions of larger inertia at the hand (Guigon et al. 2007). Access to the same motor costs for lower-level control and higher-level decisionmaking is in line with the proposal that movements are planned in parallel before final selection, e.g., Cisek and Kalaska (2010). It is unclear, however, where in the brain integration of expected cost and success occurs before the final decision to use one arm or the other. In a task in which subjects were scanned in a functional MRI while they performed a series of effortful actions to obtain secondary reinforcers, the ventral striatum and anterior cingulate cortex were shown to be involved in effort-based, cost-benefit valuation (Croxson et al. 2009). In this task, efforts were not biomechanical per se; however, instead, in the “effort phase,” subjects were required to hit targets by moving a cursor to the target position using a trackball mouse. In a simple-choice reaching task, similar to ours, transcranial magnetic stimulation (TMS) over the left parietal cortex reduced the probability of choosing the right arm by biasing the competitive process between the two arms (Oliveira et al. 2010). A recent study using TMS suggests that the primary motor cortex is involved in the computation or prediction of the biomechanical costs in choosing to move to one of two targets (Cos et al. 2014). Such involvement of the motor system in the computation of biomechanical effort makes sense, given that effort computation or prediction requires access to movement-related kinematic and dynamic variables.

Our results showing that subjects take into account target-dependent, expected success rates in arm choice are in line with a previous arm-choice experiment, in which the rate of reaching success was manipulated: subjects shifted the angle of equiprobable right/left-arm choice in the direction of the comparatively less-rewarded arm (Stoloff et al. 2011). Change in arm choice was well accounted for by a difference between expected rewards, updated via reward-prediction errors (Sutton and Barto 1998). In our study, seven subjects (out of 12) in the small-target condition appeared sensitive to these direction-specific differences, as they showed a target-specific, success-dependent modulation in right-arm use (see Table 2). In addition, subjects with similar overall success rates for the two arms showed almost no handedness bias, as captured by the near-zero constant of the logistic-regression models (see Fig. 5). In contrast, those subjects with large, overall right-hand success rates compared with overall left-hand success rates showed a nonspecific, increased use of the right hand, as captured by the positive constant in the logistic-regression models (see Fig. 5). Such nonspecific handedness bias was present even for the large-target condition of our experiment (see how the dominant right-arm choice is >50% for almost all targets in Fig. 2A). Whereas ensuring higher success overall, such “nonuse” of the left arm as a default strategy comes at the price of increased motor costs, as use of the right hand in the second and fourth quadrants requires much greater effort (see Fig. 2).

Our study has several limitations and leaves a number of open questions that need to be addressed in future work. First, to avoid collisions between the arms, we, like others (Coelho et al. 2013), translated the actual workspaces toward a middle visual target to create a collision-free visual workspace (see Fig. 1). In this experimental design, vision and proprioception are therefore not aligned. However, the difference between the actual arm posture and a visually shifted arm posture is relatively small; for instance, we estimated that the difference in the direction of the inertial ellipse at the hand between these two postures is only 18°. Second, we let subjects experience the horizontal movements, with both arms holding the robotic manipulandum, before making a choice. Therefore, it is notable whether subjects 1) estimated the costs before each decision, based on internal simulations, for instance, via simulated movement plans and inverse dynamics (Gandrey et al. 2013; Gentili et al. 2004); 2) learned the expected costs before or during the experiment (including in the familiarization session), for instance, via “cost-prediction errors”; or 3) both, as it has been proposed in reward-based choices (Daw et al. 2005). In the target-choice experiment of Cos et al. (2011), the effects of biomechanics on choice were already present at the start of the session, and it was thus argued that learning about biomechanical costs in decisionmaking occurred at an earlier stage of development (Cos et al. 2013).

Our results may shed light on choice in patients with (mostly) unilateral impairments following stroke. Although a large number of patients with stroke still retain (or regain after spontaneous recovery or rehabilitation) some function of the arm and hand, they may not use their affected arm in daily activities, e.g., Han et al. (2013), Hidaka et al. (2012), and Wolf et al. (1989). A number of factors have been proposed to account for such nonuse (Andrew and Stewart 1979), such as pain, limited range of motion, as well as higher effort for successful use of the impaired hand (Sunderland and Tuke 2005). Here, we propose that intrinsic biomechanical properties and end-point accuracy also influence limb choice and use. In addition, our novel method of predicting arm choice via logistic regression of a weighted sum of expected effort and success uncovered a handedness bias that was correlated with the overall difference in success between the right and the left hand, as predicted by learned, nonuse theories. As performance of the more-affected hand poststroke is low compared with that
of the less-affected hand, this bias could become high in individual poststroke and thus lead to near-complete nonuse of the affected arm. Such bias may be linked to “learned nonuse” (Taub 1994), as it would develop either after unsuccessful, repeated attempts to use the affected arm and hand or after negative consequences, such as spilling hot coffee. Therefore, our results provide a baseline against which arm choice in individuals’ poststroke can be compared.

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AUTHOR CONTRIBUTIONS
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