Effort, Success, and Non-use

Determine Arm Choice

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Abstract

How do humans choose one arm or the other to reach single targets in front of the body? Current theories of reward-driven decision making 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 comprised of 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 non-use in individuals post-stroke.

Keywords: motor control; reaching; decision making; motor cost; motor effort.
Introduction

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; 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 term 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; Croxson 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) influence 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 further hypothesized 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 were 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; 7
females) 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 ATR 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. 14 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 ± 0.17 SD). One subject was right-handed with correction (he formerly used to be left handed, but was instructed to be right-handed). We excluded any subjects who used either hand less than 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 4 and 5 times out of 192 free choice movements, respectively.

Experimental set-up: 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 allows horizontal movements with either hand. 24 targets were equally spaced in the four quadrants every 15 degrees on a circle of 10 cm in radius from the home position (see Figure 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 and 90 degrees respectively for each subject based on the measurement of forearm and upper arm length, as shown in Figure 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 Figure 1). Vision of the arm and hands
was blocked at all times by a horizontal board mounted above the manipulandum and on which the target and cursors were projected.

Forced and choice trials in the two conditions: For each condition, the experiment was comprised of eight trial blocks. For each trial block, one target was pseudo-randomly 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 pseudo-randomly drawn and counterbalanced across trials. During these forced movements, the other arm was prevented from moving by setting a large stiffness on its robot 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 msec or less after it left the home position in the large target condition, and 300 msec or less in the small target condition (this 30 msec 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 greater than 5 cm. According to this criterion, less than 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 200Hz, 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 random factor (note, 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 pairwise contrasts with sequential
Bonferroni corrections for multiple comparisons. In the polar coordinate plots for success in
Figure 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 set-up shown in Figure 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 \(q = (q_2, q_1)\) 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: 

\[
\tilde{u}_i = T_e T_a \tilde{\tau}_1 + (T_e + T_a) \tilde{\tau}_1 + \tau_1,
\]

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 being greater than 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 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 (Figure 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):

$$p_{k,\text{right}} = \frac{1}{1 + e^{-\beta(V_{k,\text{right}} - V_{k,\text{left}})}}$$

(1)

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, the exponential terms becomes small and $p_{k,\text{right}}$ approaches 1. The probability of choosing the left arm is simply:

$$p_{k,\text{left}} = 1 - p_{k,\text{right}}$$

(2)

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 equation 1 as:

$$p_{k,\text{right}} = \frac{1}{1 + e^{-a(\langle \text{Success}_{k,\text{right}} \rangle - \langle \text{Success}_{k,\text{left}} \rangle) + b(\langle \text{Effort}_{k,\text{right}} \rangle - \langle \text{Effort}_{k,\text{left}} \rangle) + c}}$$

(3)

where, $a$, $b$, and $c$ are parameters to be estimated, and the brackets $\langle \rangle$ 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, using 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 equation (3). In addition, because reward-independent switching or perseveration are often seen in choice data, e.g., (Lau and Glimcher 2005; 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 1 if the same hand was used in the immediately preceding forced choice movement and 0 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 equation (3), with the difference that the intercept is a now random effect, i.e. each subject has its own intercept $c_i$.

We developed and selected possible choice models using a forward selection approach. We started with the simplest (base) model with random intercepts, 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 between condition, effort and success. We finally added the prior history factor to
form the final (full) model. In order 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 $\text{AIC} = -2 \times \text{LL} + 2 \times k$, where $k$ 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). It is therefore 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 to 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: $R^2 = 1- \frac{\text{LL}}{\text{LL}_0}$, where LL is the log-likelihood and LL0 is the log-likelihood of the null model (with intercept only).
Results

Arm Choice

Comparing the choice data for the right hand in the large and small target conditions (Figure 2A and 2B) 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 degrees and 38.7 degrees 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 4 targets in the 1st quadrant and for 4 targets in the 3rd quadrant (deviation contrasts $p < 0.05$, See Figure 2A, left panel), and smaller than the mean for 5 targets in the 2nd quadrant and 4 targets in the 4th quadrant. In the small target condition, choices are greater than the mean for 4 targets in the 3rd quadrant and smaller than the mean for 2 targets in the 2nd quadrant and for 4 target in the 4th quadrant (deviation contrasts $p < 0.05$, see Figure 2B, left panel).
Task success and motor cost

Task success:

As expected, reducing target size from 3cm in the large target condition to 2 cm in the small target condition reduced success rate (compare middle panels of Figure 2A and 2B; 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: right arm 87± 2%; left arm 83 ± 2%. Success rates in the small target condition: right arm 79 ± 5%; success left arm 62 ± 4%). Pairwise target-by-target comparisons show that success rates are generally higher for 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 Bonferonni 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 around 135 degrees and 315 degrees for the right arm and 45 and 235 degrees for the right arm – see Figure 2, right panels). Thus, effort is much larger for the right arm in the 2nd and 4th quadrant 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 towards the body (right arm: cost for target at 150 degrees greater than cost for target at 330
degrees, both target conditions, $p < 10^{-4}$ left arm: cost for target at 30 degrees greater than cost for target at 210 degrees, 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 to 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 to predicted right arm choice for large (top row) and small (bottom row) target conditions for three models: Left panels show results from the model including difference in expected effort and condition (model (2) in Table 1). Middle panels show results from the model including difference in expected success and condition (model (3) in Table 1). Right panels show results from the model including all significant terms (expected effort, expected success, condition, expected effort x 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 adding both expected effort and expected success significantly improves fit compared to model (1) with condition only (LRT $p < 0.0001$), adding expected effort largely increases fit (AIC = 4,667) compared to expected success (AIC = 4,805) as can be seen by comparing left and middle panels in Figure 3. In addition, prior history of arm use on the preceding force choice trial was also a predictor of choice (model (4) in Table 1, comparison with model (1), LRT $p < 0.0001$). We tested for all interactions between condition, effort, and success, with only expected effort x condition being significant (models (5) and (10)). The right column of Table 1 shows the final “full” selected model (model (10), AIC = 4,486),
which shows excellent fit between actual choice and predicted probability of choice in both conditions (Figure 3, right panels). The signs of the model parameters show that the probability of right arm choice in free choice trials is increased by: small targets, lower expected effort for the right arm than for the left arm, greater success 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 x expected effort shows that predicted effort has less of an 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. We therefore plotted the logit of the arm choice probability as a function of effort and success for the small target conditions. As expected, Figure 4 shows a near linear relationship between logit and effort and between logit and 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 Figure 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 to the left arm tend to exhibit greater use of the right arm than the left arm, regardless of effort and target location.

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 \((\text{AIC} = 4,536 \text{ vs AIC} = 4,486,\)
LRT $p < 0.0001$), suggesting that comparison of the predicted effort for both arms occurs prior to 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 results 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-Square 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 12 subjects’ arm choice was 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 was best fit by models including effort, five subjects’ with models including effort and success, and two subjects’ with models that included only success.
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 depends 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 1\textsuperscript{st} and 2\textsuperscript{nd} quadrant, but also the increase in left arm use in the 4\textsuperscript{th} quadrant compared to the 1\textsuperscript{st} quadrant, and the increase of right arm use in the 3\textsuperscript{rd} quadrant compared to the 2\textsuperscript{nd} 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 are 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 (Dounskaia 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. showed that arm choice was affected by a force field
applied on one hand via a robotic exoskeleton (Habagishi et al. 2014). 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 utilizing
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 4th 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. First, there was no vision of the cursor in our experiment
while there was full visual feedback in Coelho et al. 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/sec, whereas in Coelho
et al., the movements were rewarded if maximum hand velocity was above 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 4th 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. 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 towards the dominant hand for
all targets. An increased bias in the Coelho et al. 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 degrees, 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 prior to 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
decision making 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 an fMRI 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 is in line with a previous arm choice experiment in which the rate of reaching success was manipulated: subjects shifted the angle of equi-probable 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 twelve) 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 left part of the graph in Figure 5). In contrast, those subjects with large overall right hand success rates compared to overall left hand success rates showed a non-specific increased use of the right hand, as captured by the positive constant is in the logistic regression models (see right part of the graph in Figure 5). Such non-specific handedness bias was present even for the large target condition of our experiment (see how the dominant right arm choice is greater than 50 % for almost all targets in Figure 2A, left panel). While ensuring higher success overall, such “non-use” of the left arm as a default strategy comes at the price of increased motor costs, as use of the right hand in the 2nd and 4th quadrant requires much greater effort (see Figure 2 right panels).

Our study has several limitations and leaves a number of open questions that need to be addressed in future work. First, in order to avoid collisions between the arms, we, like others (Coelho et al. 2013), translated the actual workspaces towards a middle visual target to create a collision-free visual workspace (see Figure 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 degrees. Second, we let subjects experience the horizontal movements with both arms holding the robotic manipulandum before making a choice. It is notably 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”, 3) or 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 of biomechanical costs in decision-making 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; Wolf 1989). A number of factors have been proposed to account for such non-use (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 endpoint 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 non-use theories. As performance of the more affected hand post-stroke is low compared to that of the less affected hand, this bias could become high in individual post-stroke and thus lead to near complete non-use of the affected arm. Such bias may linked to “learned non-use” (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 a hot coffee. Our results therefore provide a baseline against which arm choice in individuals post-stroke can be compared.
Acknowledgements:

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References


Mixed Effects Logistic Regression Results

**Dependent variable: Right Arm Choice**

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| p<0.01, p<0.001, p<0.0001

Table 1: Results of mixed logistic regression model.

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Note: p<0.01, p<0.001, p<0.0001

Table 2: Individual model fit. Top: large target condition. Bottom: small target condition. The x sign for subjects 3 and 12 in the large target condition indicates that no models fit the data (chi-square test).

Figure Legends:
Figure 1. Experimental set-up. The visual targets are shown in red. The actual movements of each arm are, however, to the targets shown in light blue. The hand positions are thus translated visually, such that the cursors indicating hand positions are seen by the subject in the center of the filled red target (home target) when the hands are at their resting positions.

Figure 2. Right arm choice, as well as success rates and estimated effort for both hands for large (A) and small (B) target conditions. Left panels: Right arm choice in the free condition. Dark blue line: mean choice probability over all subjects. Light blue shading: standard error of choice probability. Thin black line: ellipse fitted to mean choice data. + or – signs indicate that choice for this target is greater or lower than mean choice over all targets (in each condition), respectively. Middle panels: left and right success rates (mean and standard error for each hand). Blue stars (*) indicate that the right arm success rate is higher than the left arm success rate, red stars (*) the opposite. Right panels: left and right estimated effort (mean and standard error for each hand). Choice is computed from the 8 movements to each target with in free movements. Success rate and effort are computed from the 8 movements to each target with each arm in the left and right forced movements.

Figure 3: Predicted mean probability of arm choice (green line) vs actual mean probability arm choice (blue line) in large (A) and small (B) target conditions for three models (from left to right). Left column: Model with difference in expected effort and condition (model (2) in Table 1). Middle column: Model with difference in expected success and condition (model (3) in Table 1). Right column: Model with difference in expected effort, difference in expected success, condition, and history of previous movement (model (10) in Table 1).
Figure 4: Relationships between logits and difference in effort (A) and difference in success (B) for the small target condition for the full model (model (10), in Table 1). The model predicted, for each target, both a linear relationship between logits and difference in expected effort and difference in expected success.

Figure 5: Random intercept (handedness bias) of the mixed effects logistic regression model (model (10) in Table 1) as a function of the average difference in success rates between right and left arm over all targets for all subjects. The average success rates were computed in the forced trials for both left arm and right arm movements.
A: Large targets

B: Small targets
Logit vs Effort

Right Minus Left Effort

Logit vs Success

Right Minus Left Success Rate
$R^2 = 0.582$

$P = 0.0028$