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A Representation of Effort in Decision-Making and Motor Control

Highlights

- In reaching, like walking, there is a movement speed that minimizes energetic cost
- Reward makes it worthwhile to be energetically inefficient
- Effort may be represented objectively via energetic cost and discounted in time
- Neural control of decisions and movements may share a common utility

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In Brief

Both decisions and movements are influenced by reward and effort, suggesting that they may share a common utility. Shadmehr et al. demonstrate that a utility in which effort is objectively represented as energetic cost and discounted in time can account for both the choices animals make and the vigor of their movements.



A Representation of Effort in Decision-Making and Motor Control

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SUMMARY

Given two rewarding stimuli, animals tend to choose the more rewarding (or less effortful) option. However, they also move faster toward that stimulus [1–5]. This suggests that reward and effort not only affect decision-making, they also influence motor control [6, 7]. How does the brain compute the effort requirements of a task? Here, we considered data acquired during walking, reaching, flying, or isometric force production. In analyzing the decision-making and motor-control behaviors of various animals, we considered the possibility that the brain may estimate effort objectively, via the metabolic energy consumed to produce the action. We measured the energetic cost of reaching and found that, like walking, it was convex in time, with a global minimum, implying that there existed a movement speed that minimized effort. However, reward made it worthwhile to be energetically inefficient. Using a framework in which utility of an action depended on reward and energetic cost, both discounted in time, we found that it was possible to account for a body of data in which animals were free to choose how to move (reach slow or fast), as well as what to do (walk or fly, produce force F1 or F2). We suggest that some forms of decision-making and motor control may share a common utility in which the brain represents the effort associated with performing an action objectively via its metabolic energy cost and then, like reward, temporally discounts it as a function of movement duration.

RESULTS

Love goes toward love as schoolboys from their books.
But love from love, toward school with heavy looks.
—William Shakespeare

Suppose you are at the airport awaiting arrival of a passenger. As you scan the arrivals, you decide which person is your destina-

tion, and then walk to greet them. In this thought experiment, you will likely walk faster if the passenger is your child, rather than a colleague.

Our concern here is to describe a framework to account for both decision-making (which stimulus to acquire) and motor control (how fast to move). To do so, we need to consider the interaction between reward and effort. Let us consider the possibility that the brain represents effort objectively, via the energetic cost of the action.

We measured the rate of metabolic energy expenditure during reaching \dot{e}_r as a function of distance d and found that as reach duration T increased, \dot{e}_r decreased, approaching a non-zero asymptote (Figure 1A):

$$\dot{e}_r = am + b \frac{md^i}{T} \quad (\text{Equation 1})$$

In the above equation, m is effective mass of the arm (Supplemental Mathematical Derivations). If we integrate Equation 1 with respect to T , we arrive at an estimate of the energy expended to reach distance d :

$$e_r = amT + b \frac{md^i}{T^{i-1}} \quad (\text{Equation 2})$$

This finding illustrates that the energetic cost of reaching is convex in time and that there exists a reach duration that minimizes the cost. The energetics of walking a distance d are similar to that of reaching [8]:

$$e_w = amT + \frac{bmd^2}{T} \quad (\text{Equation 3})$$

Therefore, for both human walking and reaching there exist optimum speeds of movement that minimize the energetic cost. In contrast, an optimal duration does not exist if we assign a cost that depends on the integral of squared forces (Supplemental Mathematical Derivations), because in that case the cost is proportional to m^2/T^3 .

However, minimizing energy expenditure cannot be the only concern of the nervous system (Supplemental Mathematical Derivations), as evidenced by the fact that reward modulates movement speed [1–5]. To incorporate the effect of reward, consider reaching for food that has reward value $\alpha > 0$. Passage of time discounts reward, $\alpha/(1 + \gamma T)$, where γ determines how rapidly reward is discounted [9, 10]. If we view duration of the movement as an implicit delay in the acquisition of reward [11],

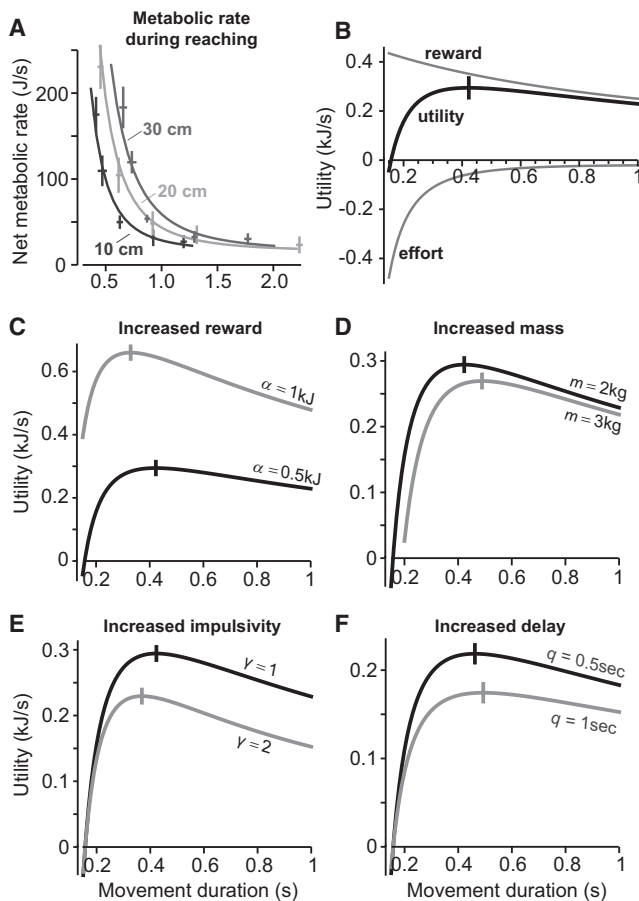


Figure 1. The Effects of Reward, Effort, and Time on Decision-Making and Movement Vigor

(A) Rate of metabolic energy expenditure during reaching as a function of reach duration for different distances. Fit to Equation 1, $R = 0.99$, $a = 15 \pm 4.8$ J/s/kg ($p < 10^{-2}$), $b = 77 \pm 16$ ($p < 10^{-3}$), $i = 1.1 \pm 0.2$ ($p < 10^{-3}$), and $j = 2.7 \pm 0.4$ ($p < 10^{-4}$). Error bars indicate the SEM.

(B) Temporally discounted reward and metabolic cost of movement, plotted as a function of movement duration ($\alpha = 0.5$ kJ, $d = 0.1$ m, $m = 2$ kg, $\gamma = 1$).

(C) With increased reward, the utility of the movement increases and the optimal duration shifts to a smaller value. As a result, a stimulus that promises greater reward carries a greater utility and also produces movements that have greater velocity.

(D) The effort of the movement is increased by increasing the mass of the limb. This decreases the utility, but also shifts the optimal duration, thereby decreasing the velocity of the resulting movement.

(E) Increasing the rate of temporal discounting decreases the utility and shifts the optimal duration to a smaller value, thereby increasing movement velocity.

(F) Increased inter-trial delay decreases the utility of the movement and shifts the optimal duration to a larger value, thereby decreasing movement velocity. Therefore, although increased inter-trial delay and rate of temporal discounting both decrease utility of the movement, the former decreases movement vigor and the latter increases it.

See also Table S1.

then the act of moving fast or slow is a decision between acquisition of a large reward soon in exchange for payment of large effort and acquisition of smaller, discounted reward later in exchange for payment of small effort. We represent effort with

function $U(T)$ and write the utility of the movement as the sum of reward and effort:

$$J = \frac{\alpha}{1 + \gamma T} + U(T). \quad (\text{Equation 4})$$

For reaching, we arrive at the following representation of effort:

$$U(T) = -\frac{amT + bmd^i/T^{i-1}}{1 + \gamma T}. \quad (\text{Equation 5})$$

The resulting utility is plotted in Figure 1B. A fast movement results in small discounting of reward but requires larger effort. A slow movement requires a small effort but will produce large discounting of reward. The maximum utility is achieved at the optimum movement duration. Equation 4 makes four predictions: as reward increases, the utility of the movement increases, but its optimum duration decreases (Figure 1C). Animals should not only prefer stimuli that promise greater reward [12], but also move with greater speed toward them [1, 2, 4, 5]. As the metabolic cost of the movement increases, the utility of the movement decreases, but its duration increases (Figure 1D). Animals should not only prefer to move toward stimuli that require lower energetic cost, but move with greater speed toward them. As time discounts reward more steeply (larger γ), both the utility of the movement and its optimum duration decrease (Figure 1E). Individuals that are more impulsive should not only prefer the immediate reward, but also move faster than individuals who are more patient [13]. Finally, if we make someone wait period q before allowing them to make a movement, we are altering the time to acquisition of reward, extending it to $T + q$. The utility becomes

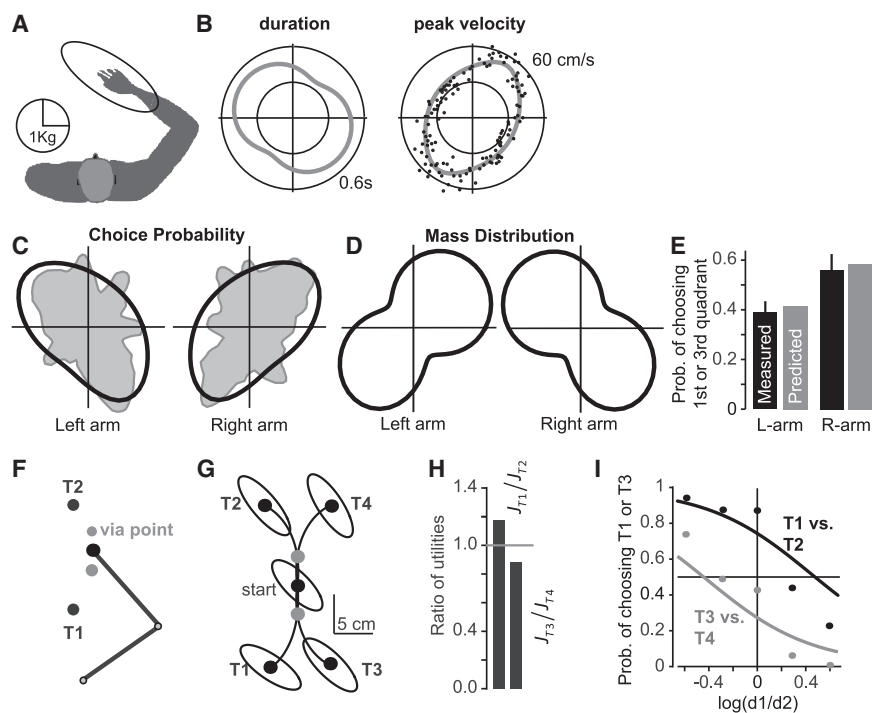
$$J = \frac{\alpha - amT - bmd^i/T^{i-1}}{1 + \gamma(T + q)}. \quad (\text{Equation 6})$$

As the imposed delay increases, movement duration also increases (Figure 1F). As a result, subjects would rather not wait to move toward a rewarding stimulus, but, if forced to do so, they will move slower [14].

We chose a utility in which effort additively combined with reward. In contrast, in previous approaches, reward and effort were combined multiplicatively [15–18]. A utility in which reward is multiplied by a function of effort is inconsistent with the observation that reward modulates movement speed (Supplemental Mathematical Derivations). We chose a utility in which time discounted effort and reward hyperbolically. Exponential temporal discounting fails to predict the effect of time delay on movement speed (Supplemental Mathematical Derivations).

A Common Utility for Some Forms of Decision-Making and Motor Control

Our framework should be able to predict the choice of which movement to perform, as well as the speed of the chosen movement. The arm has a mass distribution that resembles a heavy object when it moves in some directions (Figure 2A, major axis of the ellipse) and a light object when it moves in other directions. In [19], subjects reached without time constraints and chose a peak velocity that was around 55 cm/s for some directions, but only 35 cm/s for other directions (Figure 2B). We used the inertial properties of the arm to estimate its effective mass as a function



(G) The effective mass of the arm at the start position and at each of the various targets.

(H) The ratio of the utilities for targets T1 and T2, and targets T3 and T4, when all targets are 11 cm from the start point.

(I) The probability of choosing target T1 (or target T3) as a function of the log of the ratio of the distances for targets T1 and T2 (or targets T3 and T4). The curves are probabilities computed from the differences in utilities of the two targets.

See also [Table S1](#).

of reach direction ([Supplemental Mathematical Derivations](#)), resulting in $m(\theta)$, where θ is direction of reach. Using Equation 4, we computed the duration that maximized the utility for each direction ([Figure 2B](#)). The resulting peak velocity was largest for the directions of smallest effective mass ([Figure 2B](#); $R = 0.83$, $p < 10^{-34}$).

Volunteers were asked to reach but were not provided with a target [20, 22]. Rather, they were given the freedom to choose their own direction of movement ([Figure 2C](#)). We found that movement utility was a reasonable predictor of the distribution of directions that people had chosen ([Figures 2D and 2E](#); right, $R = 0.67$, $p < 10^{-8}$; left, $R = 0.68$, $p < 10^{-9}$).

Volunteers chose from two targets [21]. A via point was placed between the start position and each target, thereby constraining the reach trajectory ([Figure 2F](#)). This made it so that part of the trajectory was aligned with the major or minor axis of the mass ellipse. For example, consider a trial in which the options were targets T1 and T2, each placed at a distance of 11 cm from the start location ([Figure 2G](#)). Approaching T2 from the via point requires moving the hand along the major axis of the mass ellipse, whereas approaching T1 requires moving the hand along the minor axis. Because the effective mass of the arm is higher along the trajectory toward T2, its utility is lower. As a consequence, people should prefer to reach toward T1. We used Equation 4 to estimate the utility of each reach. The resulting ratio of utilities for targets T1 and T2, represented as J_{T1}/J_{T2} , and targets T3 and T4, represented as J_{T3}/J_{T4} , are shown in [Figure 2H](#). As the dis-

tance to targets T1 and T3 increased, the preference shifted to targets T2 and T4 ([Figure 2I](#)).

In summary, if we define utility of an action as the temporally discounted sum of reward and effort, where effort is the energetic cost of the movement, then we may account for both movement vigor and movement choice across a few reaching experiments.

Temporal Discounting of Effort: Walking versus Flying

Starlings chose whether to walk or fly to obtain reward [23]. The value of reward was the caloric content of the food, and the metabolic costs of flying e_f and walking e_w were measured (flying required about 15 times more energy than walking). The birds chose between making multiple flying trips to receive reward and making multiple walking trips (to a closer site) to receive the same reward. On the final trip, the birds obtain the reward. For a fixed number of flying trips n_f , the number of walking trips n_w was incremented until a preference reversal was observed, indicating an indifference point ([Figure 3A](#)). Using Equation 4, we calculated the utility of each option. The utility of making n_w walking trips is

$$J_w = \frac{\alpha - e_w(n_w)}{1 + \gamma T_w(n_w)}. \quad (\text{Equation 7})$$

To compute indifference points, we set $J_w(n_w) = J_f(n_f)$ and solve for n_w . The only free parameter is γ . In this experiment,

Figure 2. Effort Representation via Metabolic Cost May Account for Both the Decision of Which Movement to Make and the Speed of the Ensuing Movement

(A) The configuration of the arm at the start position and the associated effective mass $m(\theta)$. In this configuration, the greatest mass is associated with movements to targets aligned with the forearm and is three times the mass in the perpendicular direction.

(B) Subjects were instructed to reach to a target at 10 cm with no time constraints [19]. The resulting peak velocity as a function of direction is plotted as dots. The gray curve shows predictions of the utility function, where effort is objectively measured via metabolic cost of the reach ([Figure 1A](#)).

(C) Subjects performed an out-and-back movement but were free to choose the reach direction (no target provided). The gray region shows the probability distribution of the observed choices [20]. The black curve is the prediction.

(D) The mass matrix for an out-and-back movement as a function of reach direction for the left and right arm.

(E) Probability of choosing to reach toward first or third quadrant. Error bars indicate the SD.

(F) Subjects were presented with two targets [21] and chose to reach to one of the targets, moving their hand through a via point.

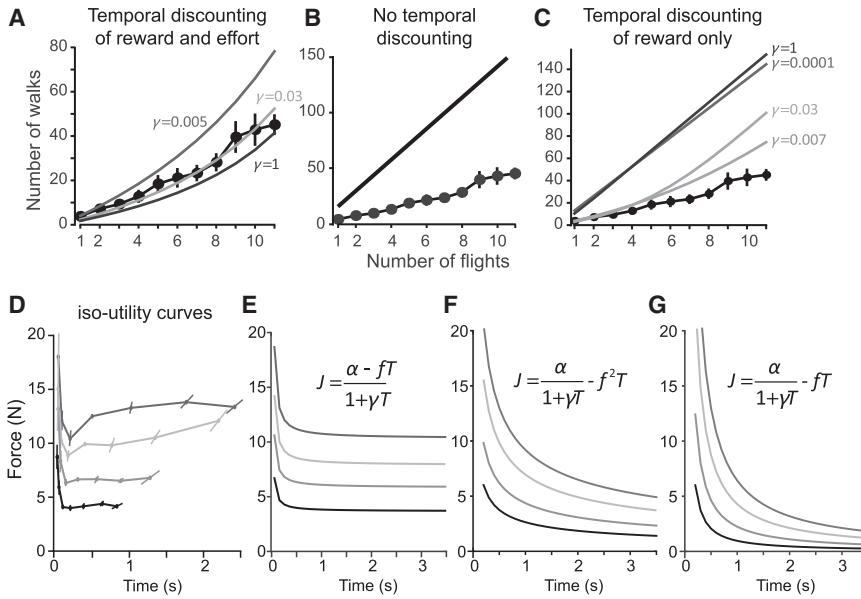


Figure 3. Decision-Making in Birds and Humans

(A) Birds chose between flying a number of times and walking a number of times to receive a constant reward. The data points represent the indifference values [23]. Error bars indicate the SEM. The solid curves are the predicted indifference curve for the utility function in which both reward (energetic content of the food) and metabolic cost are discounted by time. The effect of γ , the only unknown parameter in the model, is a monotonic change in the indifference curve.

(B) Predictions of a utility in which neither reward nor metabolic cost are discounted by time. There are no free parameters.

(C) Predictions of a utility in which only reward is discounted by time. The effect of γ is a non-monotonic change in the indifference curve and the optimal value produces a poor fit to the data. (D) Iso-utility curves for a force production task [24], where each curve connects the force-time pairs that were judged to be equally effortful. For durations of greater than 0.5 s, force held for a short amount of time was judged to be approximately equal in effort to the same force magnitude

held for a longer amount of time. Error bars indicate the SEM.

(E) The iso-utility curves predicted by an effort cost in which the metabolic cost of force production (force-time integral; see Figure S1) is discounted as a hyperbolic function of time. The function reaches a plateau as the duration of force production increases.

(F) The indifference curves predicted by an effort cost that depends on the integral of the squared force (as is typical in optimal control models). The function goes to zero with increased duration.

(G) The indifference curves predicted by an effort cost that does not temporally discount the force-time integral. The function goes to zero with increased duration. See also Figure S1 and Tables S2 and S3.

where the value of reward and effort were objectively known, the model's performance was an excellent match with the decisions that the birds had made ($R = 0.99$, $p < 0.0001$).

Now consider a scenario in which reward and effort are not temporally discounted, $J_w = \alpha - e_w(n_w)$. This predicts that the birds should take many more walking trips than observed (Figure 3B). Alternatively, consider a scenario in which only reward is discounted,

$$J_w = \frac{\alpha}{1 + \gamma T_w(n_w)} - e_w(n_w). \quad (\text{Equation 8})$$

Here, the effect of γ on the indifference curve is non-monotonic, grossly over-estimating the measured data (Figure 3C).

In summary, when the values of reward and effort were known via their energetic contents, a utility in which effort is represented via temporally discounted movement energetics accounted for the decisions that birds made in flying versus walking.

Temporal Discounting of Effort: Isometric Force Production

The metabolic cost of producing an isometric force $f(t)$ for duration T is (Figure S1)

$$e = a_1 \int_0^T |f(t)| dt + a_2. \quad (\text{Equation 9})$$

When one is asked to produce a constant force F for period T , the utility of this action is

$$J = \frac{\alpha - a_1 FT - a_2}{1 + \gamma T}. \quad (\text{Equation 10})$$

The effort is

$$U = -\frac{1}{1 + \gamma T} (a_1 FT + a_2). \quad (\text{Equation 11})$$

The above result makes the surprising prediction that as duration of force production increases, effort reaches an asymptote. That is, as duration of action increases, subjects become increasingly indifferent to duration.

Volunteers produced F_1 for T_1 , and then F_2 for T_2 [24]. They chose which force-time pair they would like to experience again ("choose the force-time pair that you judge to be less effortful"). By increasing F_2 , the authors determined the indifference point and observed that the iso-utility curves reached a plateau with increased duration (Figure 3D). Our theory provides an explanation. We solved the equality $J(F_1, T_1) = J(F_2, T_2)$ for F_2 , arriving at the following expression for the iso-utility curve:

$$F_2 = \frac{\gamma(\alpha - a_2)(T_1 - T_2) + a_1 F_1 T_1 (1 + \gamma T_2)}{a_1 (1 + \gamma T_1) T_2}. \quad (\text{Equation 12})$$

As $T_2 \rightarrow \infty$, F_2 reaches an asymptote that depends on F_1 (Figure 3E; $R = 0.92$, $p < 10^{-11}$). In contrast, let us consider existing models in which effort is represented as the undiscounted sum of squared forces. In that case,

$$J = \frac{\alpha}{1 + \gamma T} - aF^2 T. \quad (\text{Equation 13})$$

The iso-utility curves become

$$F_2^2 = \frac{F_1^2 T_1}{T_2} - \frac{\alpha}{aT_2(1 + \gamma T_1)} + \frac{\alpha}{aT_2(1 + \gamma T_2)}. \quad (\text{Equation 14})$$

As $T_2 \rightarrow \infty$, $F_2 \rightarrow 0$ (Figure 3F), a fact inconsistent with measurements [24]. Indeed, this inconsistency remains whether forces are quadratically penalized or not (Figure 3G).

In summary, if we represent effort as the temporally discounted metabolic cost of action, then the perceived effort associated with generating an isometric force does not grow unbounded as a function of duration, but rather approaches an asymptote. This counter-intuitive prediction provides the first explanation that we are aware of for empirical data regarding decisions that people made in an isometric force task.

DISCUSSION

We measured the energetic cost of reaching and parameterized it as a function of movement duration, mass, and distance. We found that energetics of reaching, like that of walking, is a convex function of time with a global minimum. This demonstrates that for both reaching and walking there are movement speeds that are energetically optimum. Indeed, people and other animals walk and reach at speeds that are near energetic minimums (Supplemental Mathematical Derivations). However, animals move faster when there is greater reward at stake [1, 5]. That is, reward makes it worthwhile to be energetically inefficient.

Earlier work had suggested that the brain may assign a utility for each potential action, where utility contains an interaction between reward and effort [6, 7]. Here, we represented effort objectively via the energy needed to produce the movement and then temporally discounted it like reward. The resulting equations made the following predictions: animals should prefer the more rewarding stimulus and move with greater vigor toward it [5]; animals should prefer the less effortful movement [21] and make that movement with greater vigor [19]; and animals should prefer not to wait before acquiring reward, but, if forced to do so, they will move with reduced vigor [14].

In our framework, effort and reward interact additively and are discounted by time. In decision-making, it is often assumed that effort discounts reward multiplicatively [15, 16, 18]. This is inconsistent with the observation that reward modulates movement vigor. In motor control, effort is represented as the undiscounted sum of squared forces [25–28]. This makes the incorrect prediction that effort grows unbounded with action duration [24]. In contrast, our results connect motor control with optimal foraging theory [29], where decisions depend on the energy gained via the reward, minus the energy spent performing the act, divided by time.

We did not consider decision-making in tasks where evidence is accumulated over time [30]. A recent study demonstrated that the urgency with which a decision is made (i.e., decision speed) affects the vigor of the ensuing movement [31]. We also did not measure the relation between mass and energetic cost of reaching. When people walk with backpack loads, energetic cost increases linearly with mass [32]. Thus, our framework assumes a linear relationship between mass and energetic cost, but this awaits experimental validation.

Our utility cannot account for certain behaviors. When people train to reach in a force field in which a straight trajectory requires more force than a curved trajectory, they choose the straight trajectory [33] (but see [27, 34, 35]). When people walk with an exoskeleton that alters the relationship between step frequency and metabolic cost, they persist on producing their now higher cost natural step frequency, until coached to explore [36]. These examples illustrate instances in which the brain chooses an action that requires greater effort, despite availability of a lower effort option.

Dopamine depletion alters the interaction between reward and effort, shifting preferences toward actions that are less effortful [37, 38]. In the striatum, dopamine interacts with medium spiny neurons (MSNs). MSNs with D1-type receptors project via the direct pathway of the basal ganglia, whereas MSNs with D2-type receptors project via the indirect pathway. Bilateral activation of MSNs in the indirect pathway reduces movement vigor, whereas stimulation of MSNs in the direct pathway increases vigor [39]. This led Hwang [40] to propose that the indirect pathway of the basal ganglia is involved in computing effort costs, whereas the direct pathway is involved in computing the expected reward. In this framework, the utility of an action may be computed via the convergence of the direct and indirect pathways at the substantia nigra pars reticulata (for control of saccades) or the internal segment of globus pallidus (for control of reaching).

Our theory provides a different way to consider experiments in which subjects are free to choose the stimulus to reach for, as well as the arm to use. A current approach asks whether the stimulus is chosen first, or the arm [41]. In contrast, our theory suggests that each potential stimulus/arm pairing is assigned a utility, and then the option is chosen that has the highest utility. Our model suggests a strong coupling between the neural circuits responsible for generating an action and the circuits involved in deciding between actions. This aligns with the hypothesis that decision-making involves sensorimotor areas, where each potential movement is represented simultaneously and competes against other potential movements [42]. The intriguing possibility is that effort is associated with an internal model of the energetic cost of action and, like reward, is discounted in time.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, mathematical derivations, one figure, and three tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.05.065>.

AUTHOR CONTRIBUTIONS

H.J.H. and A.A.A. designed, collected, and analyzed the data for the metabolics of reaching. R.S. and A.A.A. developed the mathematical framework, performed simulations, prepared figures, and wrote the manuscript. All authors approved the final version of the manuscript.

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