# ON THE INTERACTIONS OF REWARD, TIME, AND EFFORT IN HUMAN MOVEMENT

By

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ON THE INTERACTIONS OF REWARD, TIME, AND EFFORT IN HUMAN MOVEMENT

Thesis directed by Alaa A. Ahmed, Ph.D.

*Abstract*

The goal of our actions should be to maximize reward while minimizing effort and time. An individual's movements in response to changing costs and rewards can reveal how they value these contributing variables.

The motivation of this dissertation is to better understand how reward, effort, and time interact to determine an individual's movement preferences. The first study used an objective measure of effort, metabolic cost, to quantify subjective effort valuation in healthy young adults in a low-effort reaching task. Participants were idiosyncratic in how they valued effort with the group as a whole representing effort objectively. The second study investigated the costs of effort and time in gait choice by probing preferences to walk or run across changing relative distances. I found that effort alone could not explain choices. Participants also considered time, with their tendency to discount time predicting running velocity. These first two studies demonstrate that effort is essential in explaining movement behaviors with its exact contribution varying *across* individuals.

In the third and fourth studies I investigated the role of reward in discounting effort costs in movements *within* individuals. The third study consisted of young adults reaching towards alternating quadrants where some quadrants were paired with reward. Expectation of reward led participants to react earlier and move faster, discounting the cost of effort to arrive at the reward sooner. Movements toward reward were also less variable, violating the traditional speed-accuracy trade-off. For the final study, I probed whether aging would influence an individual's willingness to alter reaching behavior in response to reward. Older adults exhibited a reduced response to reward. While reward led to faster reaction times, I did not observe an increase in movement speed. I found that metabolic cost of reaching was not elevated in older adults compared to young, suggesting that the reduced response in older adults could not be explained by an increased effort cost, but rather a reduced sensitivity to reward.

Collectively, these studies advance our understanding of how reward, time, and effort interact in explaining movement preferences in changing cost and reward landscapes both within and across human populations.

# DEDICATION

To the people in my life who make it easy to wake up excited for a new day and leave me going to bed with a smile on my face. There are many of you and I appreciate each and every one.

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# INTRODUCTION

Our lives are full of situations where we pit time and effort against reward. Imagine you open the refrigerator only to find that it is empty. You are hungry and need to eat before continuing with your day. There are several solutions to this problem that require differing levels of effort for differing amounts of reward. You could walk to the restaurant down the block for a quick sandwich, or perhaps walk to the market a little further away and get groceries for the entire week. Each alternative varies both in costs, and the rewards obtained from those costs. Subsequently, once you decide on the solution to your hunger, you now need to execute the action in an optimal manner that enables you to realize the predicted outcome of your initial decision. In the case of choosing where to go, you now need to establish an appropriate speed at which to walk to your destination or, if you are really hungry, the speed at which you run.

The initial process of deciding which action to take and the subsequent process of performing that preferred action can both be fundamentally framed by pitting reward against time and effort. Traditionally, these two phenomena were probed by completely different fields with the field of economics focusing on the first process and the field of motor control focusing on the later process, with little interaction or collaboration between the two despite the shared latent variables contributing to their observations. More recently, the fields have begun to converge and new models exploiting theories from both lines of research have been proposed to probe how a single utility formed by the interactions of reward, time, and effort can be used to explain behaviors across different levels of movement and decision making.

## 1.1 Reward, time and effort in decision making and movement

A successful model used to explain decision making and movement should include an accurate and universal quantification of reward, time, and effort. In this section, I summarize methods used in measuring these parameters as well as how changes in these parameters alter decision making and movement preferences in humans and other animals.

*Reward as an incentive*

Animals move to place themselves in a more rewarding state. Because movement is a costly behavior, it is necessary to have an understanding of how reward is valued to predict decision making as well as how changes in reward can lead to changes in movement preferences. In the following paragraphs I review the different reward modalities used across a range of decision making paradigms as well as how they contribute to establishing a universal currency for movement utility.

*Reward in decision making*

The quality or availability of reward affects an animal's preference towards that reward. When given the option between a large or small reward, animals will choose the large reward (Walton et al. 2002; Levy and Glimcher 2011). Including reward into a model of utility requires that the reward be quantifiable, with changes in this quantity predicting changes in decision-making preferences. Certain rewards such as food and water are commonly quantified based on their physiological impact on an animal. For example, food can be quantified in terms of calories, water in terms of volume,

cigarettes in terms of nicotine content, etc. In the laboratory, animals adjust their decision making towards liquids with higher quantities of sucrose (Smith and Duffy 1955; Conrad and Sidman 1956) or greater numbers of food pellets (Walton et al. 2002). Smokers are able to detect differences in cigarettes, making choices that maximize nicotine content (Venugopalan et al. 2011). These results show the basic principle that the quality of a reward can be quantified based on altering characteristics of the reward that directly affect the physiology of the animal, moreover increasing these aspects of the reward, leads to an increased probability of choosing that reward.

Quantifying reward according to its physiological impact can accurately predict decision making within a single reward modality (Bautista et al. 2001), however, this method fails to predict value across modalities. For example, water could never be valued in terms of its caloric content, however that doesn't mean that quantities of water cannot be exchanged for quantities of food. Green and Rachlin (1991) trained rats to distribute a limited number of lever presses for combinations of food and water, where food was given after x presses and water after y presses. When the prices of each were altered, so too was the rat's relative spending. These results show that food and water can be valued and exchanged under a common currency. Measuring this common currency is difficult in both humans and other animals. In humans, money can be used as a good proxy, which may explain why it is the predominant reward used in human decision-making research. Money itself has no immediate effect on the physiological fitness of an individual, however it can be exchanged to acquire a large spectrum of resources and services, making it an ideal reward for human research. Levy and Glimcher (2011) had human participants choose between different amounts of money

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and either food or water rewards. They found that changes in the value of monetary rewards correlated with changes in the value of both food and water rewards. More abstract measures of a common reward currency have been recorded using neuroimaging techniques with evidence suggesting that activity in regions of the ventromedial prefrontal cortex can predict decision making across consumable and non-consumable rewards (Chib et al. 2009).

*Reward in movement*

Reward not only affects decision making, but it also influences the *vigor* in which movement decisions are executed. Vigor is commonly referred to as the peak velocity, reaction time, and duration of a movement over a fixed distance (Opris et al. 2011; Choi et al. 2014). For example, non-human primates make saccadic eye movements with shorter latencies and faster peak velocities to targets when that target is paired with a juice reward (Takikawa et al. 2002). Similar findings occur in humans when they saccade towards information rich targets (faces compared to static images) (Xu-Wilson et al. 2009). Reward dependent changes in vigor are not just constrained to saccades, but are also evident in reaching movements. In non-human animals, reward increased vigor in both simple wrist flexion/extension movements as well as reaching movements (Opris et al. 2011; Mosberger et al. 2016). It has also been proposed that reward decreases the variability in our movement. Manohar et al. (2015) reported an increase of accuracy when making saccades in the presence of distractors if the target was paired with a reward. Trommershauser et al. (2006) had individuals make rapid pointing movements to a rewarded target. When a penalty target was overlaid with the rewarded

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target, individuals adjusted their preferred pointing location away from the penalty, however when the reward was increased, they moved their preferred pointing location closer to the penalty, suggesting that they were willing to accept a new trade-off between an increased risk of penalty for an increased chance of successfully hitting the more rewarding target. These results were extended by O'Brien and Ahmed [2013] to include whole body movements. They had participants both reach and make whole body postural movements towards the edge of a cliff. They were rewarded based on how close to the virtual cliff they moved. When the consequences of the cliff were increased, participants did not move as close in either movement type. Interestingly, the effects of increasing cliff consequence was greater in postural movements compared to reaching, suggesting that the influence of reward may differ across movement types.

In this section I have presented a brief overview of how humans and other animals prefer decisions and movements that are tied with greater reward. Increasing reward also affects motor control strategies, specifically by increasing vigor. For a model of utility to function in environments that require complex decisions and/or movements, it is important that reward be represented in a common currency that can be easily quantified across a range of reward modalities.

## 1.2 Temporal discounting of reward

In the next several paragraphs, I introduce how time acts as a cost that interacts with the value of reward. A useful model of utility requires that the cost of time is accurately considered when predicting utility in both decision making and movement.

*Cost of time in decision making*

Adding a delay to a reward causes the preference towards choosing that reward to decrease (Mazur 1987). An animal's tendency for immediate rather than delayed rewards is measured in their level of temporal discounting (impulsivity). For example, both pigeons and rats consistently prefer smaller food rewards with small delays when compared to larger food rewards with a slightly longer delay. Temporal discounting varied across animals with pigeons being more impulsive than rats, willing to accept even smaller rewards to shorten the delivery of that reward (Green et al. 2004). In humans, temporal discounting of monetary reward can be observed across several timescales from (milli)seconds (McClure et al. 2007; Gregorios-Pippas et al. 2009; Haith et al. 2012) to years (Myerson and Green 1995), however, the rate at which time discounts reward depends on the scale of the delay. For example, delaying a $15 reward three months came at a much higher discount rate (277%) compared to when the delay was extended to a year (139%) (Thaler 1981).

Temporal discounting rates can also be affected by the reward modality. Differences in rates have been recorded between juice and water (McClure et al. 2007) as well as between hypothetical health outcomes and money (Chapman 1996). These results further argue the importance of a universal model of utility that can be used to explain decisions across a range of reward modalities that are delivered across a range of temporal delays.

*Cost of time in movement*

No movement is ever completed instantaneously. Execution requires muscles to create torques that accelerate and decelerate segments, all occurring over time. The rate of temporal discounting between movement initiation and completion can have an effect of establishing natural levels of vigor when moving. A reward takes longer to acquire the further away it is. The longer that a movement takes, the lesser the value of that reward as a result of temporal discounting (Shadmehr 2010). To minimize the loss of value due to temporal discounting, vigor is increased in the presence of higher initial reward. As previously mentioned, this interaction of time and reward has previously been recorded in saccades for both humans and other animals (Takikawa et al. 2002; Xu-Wilson et al. 2009), as well as in reaching with non-human animals (Opris et al. 2011; Mosberger et al. 2016).

There is evidence that the phenomena of temporal discounting in decision making and movement are linked (Shadmehr 2010). Choi et al. (2014) measured saccade vigor in healthy humans and found tremendous variability in their levels of vigor (up to 50% differences). They also used a temporal decision making task to measure each participant's rate of temporal discounting. They found that the more impulsive an individual was (higher temporal discounting), the quicker they executed their saccades.

Temporal discounting influences decision making as well as the vigor at which an animal executes movements. Increased impulsivity causes greater rate of loss in value over time, which promotes preferences towards earlier rewards in decision making. Assuming that the reward is only obtained upon movement completion, there will always be a loss between the instantaneous value of an outcome and the temporally

discounted value obtained upon movement completion. Increased impulsivity causes greater rate of loss in value over time, which promotes increased movement vigor. The basic framework of temporal discounting allows us to explain how time and impulsivity can explain differences in decision making brought on by delay as well as why certain individuals move with greater vigor than others when controlling for reward.

## 1.3 Effort discounting of reward

The classical economist David Ricardo defined price as "the value of a commodity, or the quantity of any other commodity for which it will exchange, depends on the relative quantity of labor which is necessary for its production" (Ricardo 1817). Every movement comes at a price. Very little is known about how the brain quantifies the price of effort in decision making. This is in contrast to the locomotion literature, where metabolic costs are systematically measured and thought to be one of the predominant variables determining movement (Ralston 1958; Hoyt and Taylor 1981; Diedrich and Warren 1995). Here, I present an overview of how metabolic cost is measured in animal movement, how that cost influences the way we make decisions, as well as how it affects our movements.

*Quantifying effort*

When an organism is stimulated to move, chemical potential energy is converted into mechanical energy that generates forces necessary to perform work on the environment. In the case of humans and other animals, this is done by breaking down fats, carbohydrates, and at some level proteins, to power the actions of skeletal muscles

found crossing the multiple joints of the skeleton. Across several fields of study, it is commonly agreed that the gold standard in quantifying the effort involved in movement behavior is through the magnitude of the metabolic energy required to perform the task (Margaria et al. 1963; Charnov 1976; Lemon 1991; Bautista et al. 2001). Metabolic rate has been measured for decades in locomotion using indirect calorimetry (Ralston 1958; Hoyt and Taylor 1981) however it has only recently been implemented to quantify effort in other movements like reaching (Huang et al. 2012; Huang and Ahmed 2013, 2014).

To calculate the amount of metabolic energy released by an organism, a bomb-calorimeter is used to measure the changes in heat released as a result of the catabolism of fuel (Lighton 2008). While this method is very precise, it is financially extremely expensive and sensitive to environmental changes inflicted by sources other than the organism of interest. Indirect calorimetry is a more preferred method when measuring metabolic costs in movement. This technique calculates metabolic rate (Watts) using an equation developed by Brockway (1987) where the rates that gases are absorbed (oxygen) and expired (carbon dioxide) during activity are combined to calculate the metabolic power generated from the physiological processes of the animal [eq 1.1].

$$\text{Metabolic Power (Watts)} = 16.58\, V_{O2} + 4.51\, V_{CO2} \qquad [\,1.1\,]$$

For the power obtained from indirect calorimetry to accurately reflect metabolic events at the muscle, the movement task must meet two primary assumptions. First, the task must be aerobic (Lighton 2008). Anaerobic tasks that rely on non-oxidative mechanisms cannot by detected in the analyzed expired gases. Second, the task must occur at a constant workload (speed or power) because values are obtained by averaging noisy samples over a time period of ~2-3 minutes (Donelan et al. 2001; Gottschall and Kram

2003; Grabowski et al. 2005; Huang et al. 2012)**.** Under these methodological constraints, quantifying effort in terms of exact metabolic rate has predominantly been recorded in a select category of movements, primarily behaviors that include walking, running, and cycling**.**

The speed at which a movement occurs has an immediate effect on the metabolic rate of the animal. As locomotion speed increases, so to does the metabolic rate of the organism, however, the function describing that increase depends on how fast the individual is moving. In walking, metabolic rate increases with velocity squared, while in running, it increases linearly with velocity (Ralston 1958; Margaria et al. 1963). In higher speed activities such as in cycling, metabolic rate increases with cubed velocity due to interactions with drag forces, however, when this cost is described as a function of mechanical power, the response becomes linear (Gaesser and Brooks 1975; Davies 1980). Metabolic rate also increases with the mass of an organism (Nagy 1987). When external loads are added to humans, the metabolic rate of walking increases linearly with the slope depending on the location of the added mass (more distal=more costly) (Browning et al. 2006). There is new evidence that increasing reaching distance and decreasing reaching time (increasing velocity) also lead to increases in the metabolic rate of reaching (Shadmehr et al. 2016), however compared to walking, further work needs to be done to understand how the relative components of a reaching movement (acceleration, braking, weight support, etc.) each contribute to the metabolic rate of reaching.

*Effort in decision making*

Effortful tasks are commonly used as independent variables in decision-making research (Mitchell 1999; Goble et al. 2007; Floresco et al. 2008; Prévost et al. 2010). These tasks tend to be shorter in duration and/or demand extreme (both low and high) levels of exertion meaning indirect calorimetry is not an option for measuring effort. Several proxies for effort have been proposed that when manipulated, result in changes in decision making behaviors. They include movement repetition, grip force, and mass.

Movement repetition, most commonly quantified by button or lever presses is one rudimentary proxy for effort that can easily be applied to both human and non-human paradigms. When controlling for reward, increasing the number of repetitions required in a decision leads to an increased frequency of switching to the alternative, less effortful option (Floresco et al. 2008; Croxson et al. 2009). A concern with this proxy is that there is also an uncontrolled temporal cost that interacts with effort where higher effort tasks (more repetition) also require more time to complete (Croxson et al. 2009).

An alternative proxy of effort can be quantified by altering the amount of force involved in a motor task. Studies that use isometric handgrip tasks quantify effort by measuring the amount of force an individual can generate during a maximum voluntary contraction (MVC). In these studies, participants make effortful decisions according to a percentage of MVC generated for a discrete period of time, with individuals preferring low versus high levels of contraction (Mitchell 1999; Prévost et al. 2010; Hartmann et al. 2013). Kording et al. (2004) measured how force represented effort using a decision making task where participants held the handle of a robot as it generated force pulses of differing magnitudes and durations. They then reported preferences between pairs of

effortful bouts varying in force magnitude and duration. They found that effortful decisions could be consistently predicted across individuals as the integral of force with respect to time. This trend similarly represents how metabolic cost rises with force in single muscle isometric force generation (Kushmerick M J and Paul R J 1976). Unfortunately, the forces generated by muscles during these force tasks do not allow for the disentangling of co-activation between agonist and antagonist muscles and therefore do not allow for a direct translation between force and metabolic cost.

Effort can also be modulated by changing the direction of a reach. The direction of the reach and the relative contributions of the joints to displace the hand result in different levels of inertia, or effective mass. The inertia of the arm is such that reaching in certain directions feels like moving a heavy mass, while reaching in other directions feels like moving a mass that is only half as heavy. In other words, the effective mass of the arm varies as a function of movement direction. For reaches of the right hand, effective mass is minimized along movements towards the upper right (45 degrees from horizontal) and lower left (225 degrees) planes. Goble et al. (2007) instructed individuals to distribute strokes in as many different directions as possible around a center target. They found that there was a large bias in strokes towards paths that minimized effective mass. Adding a load to the arm further increased the bias (Wang and Dounskaia 2012). Cos et al. (2014) had individuals make decisions to reach towards one of two different targets of equal distance. Again, different locations of the targets meant there were different effective masses of the arm, with participants preferring target directions that minimized this mass.

Proxies for effort such as movement repetition, grip force and mass are simple, easily controlled movements with a large range of effort levels that allow us to thoroughly probe how decision-making behavior responds to varying levels of movement exertion.

*Effort in movement*

Effort plays a role not just in decision making, but also in how we generate movement. An extensive body of work on the energetics of walking has allowed us to probe how preferred walking kinematics correlate directly with objectively measured metabolic minimums. At a walking speed of 1.45 meters per second, the legs move at a step width of ~0.12 times the length of the leg (Bauby and Kuo 2000) as well as a stride length of ~1.3 meters (Danion et al. 2003). Donelan et al. (Donelan et al. 2001) measured the metabolic rate for walking at a natural step width, then constrained participants to walk with both narrower (up to 0.1 times leg length narrower than preferred) and wider (up to 0.45 time leg length longer than preferred) step widths. They found that narrowing and widening step width increased net metabolic rate by up to 45%. Gordon et al. (2009) performed a similar experiment, but instead constrained stride length between 0.6 and 1.2 of preferred stride length. As with step width, they found metabolic cost of transport to be minimized at preferred length with increased net metabolic rate (up to 114%) at both shorter and longer stride lengths. When locomotion kinematics are perturbed from their preferred level, metabolic rate increases, supporting the hypothesis that minimizing effort is important in explaining preferred movement behaviors.

In reaching movements, effort is commonly approximated as the sum of squared forces (Todorov and Jordan 2002; Izawa et al. 2008). The sum of forces is not directly measured, but is instead calculated using inverse dynamics. This approximation is largely due to mathematical convenience, as well as the fact that metabolic costs associated with reaching movements had not been measured until recently (Shadmehr et al. 2016). When these costs were measured, the data revealed that metabolic rate decreased with increasing movement duration and increased with mass, indicating that for a movement of a given distance, faster movements generally cost more than slower movements and moving greater mass costs more than moving less mass. Thus by reducing the speed of the movement, the cost of moving a given mass can be reduced. There is experimental data supporting such an effect of mass on preferred reach speed. Gordon et al., (1994) asked subjects to make 10cm reaching movements to targets placed on the perimeter of a circle. They found that reach vigor varied as a function of reach direction with faster reaches occurring in directions that involved moving less effective mass, and slower reaches occurring in directions that involved moving more effective mass.

In this section I have provided a wide, but not all encompassing review of how effort is quantified across decision making and movement. Quantifying effort as metabolic cost can explain natural walking preferences such as stride length and step width, however, directly measuring metabolic cost is not conducive for most movements used in decision making tasks. Proxies developed in place of metabolic cost allow for investigations into how effort drives decision making. Recent developments in the methodology of indirect calorimetry have allowed us to measure metabolic rate in

reaching. With a metabolic quantification of effort in reaching I have been able to test the validity of several proxies, supporting the use of some (force) and questioning the assumptions of others (squared force).

## 1.4 A utility for decision making and movement

In the following paragraphs I present evidence that individuals subjectively distort the value of rewards and costs and that these distortions, when properly quantified, can explain changes in both decision making and movement behavior. The extent of distortion in these parameters can be used to help explain variability in behavior in animals spanning different species, age, and health.

*Models of reward*

Economists have long observed that the value of reward does not increase linearly with a discrete change across different baseline magnitudes (Bernoulli 1954). For example, the difference between receiving a single additional liter of water when you previously only had two carries a much more noticeable change in utility compared to the exact change of one liter when you already have ten (Figure 1.1).
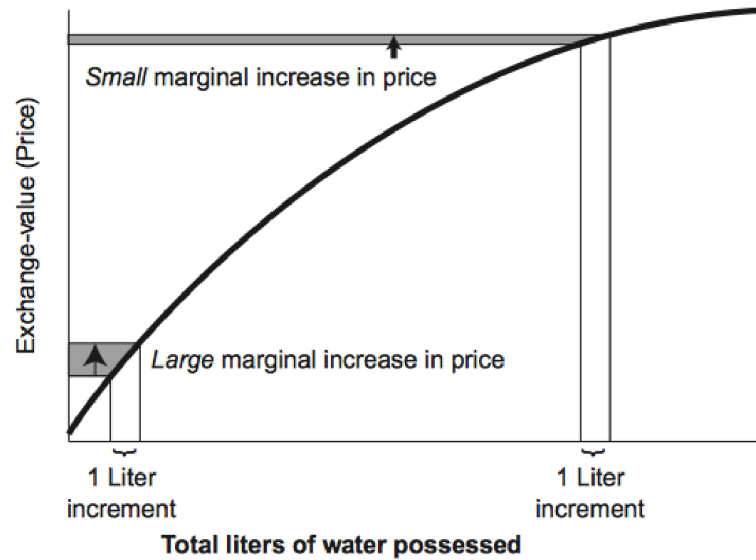
Figure 1.1 Diminishing marginal utility. A discrete increase in the quantity of a reward results in non-linear changes in utility (value) depending on your state preceding the change. Adapted from Glimcher and Fehr (2014).

This observation is referred to as the *law of diminishing marginal utility* and has consistently been observed in both humans and other animals for centuries (Menger 1871). Explaining how the value of a reward changes with magnitude can be described by fitting an exponent to a power function:

$$SV(R) = R^{\alpha} \qquad\qquad [\,1.2\,]$$

Here the subjective value of reward SV(r) is represented by a fitted exponent ($\alpha$) to an objective measure of the reward. If a fitted $\alpha$ is less than one (predicted by diminishing utility), a discrete change in reward at higher magnitudes has a lesser effect on utility than a similar change at lower magnitude. Alternatively, an exponent greater than one suggests the opposite with discrete changes at higher magnitudes having greater effects on utility compared to at low magnitudes. Lastly, an exponent around 1 suggests that changes in reward are valued equally across magnitudes. Fitting the exponent that

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describes the subjective value of reward is achieved through the use of lotteries where participants record their preferences between certain smaller rewards and larger rewards that are associated with a probability of receiving that reward or an alternatively less desirable outcome.

*Models of reward to predict decision making:*

Imagine someone approaches you and presents an offer. They will either give you a dollar on the spot, or at the flip of a coin, give you two dollars if you win and zero if you lose. Statistically, these two prospects are of equal value, however you preference towards one outcome says something about the manner in which you subjectively value increasing reward.

Levy and Glimcher (2011) used a design similar to this example to measure how the subjective value of different rewards (food, water, money) changed across different magnitudes. They found that participants generally exhibited diminishing marginal utility across all rewards (exponents less than one). Furthermore, they reported that the extent that these rewards were subjectively valued was very similar across all modalities. Subjective valuation of reward has been measured in other animals as well. Yamada et al. (Yamada et al. 2013) compared the level of subjective valuation between humans and monkeys and found that monkeys subjectively discount rewards in a manner similar to humans.

*Models of reward to predict movement:*

The subjective valuation of reward can also be measured in movement. This can be done using similar methods as in decision making, but instead of lotteries being presented explicitly as percentages, they are manipulated by having the chance of success modulated normalized to the implicit movement variability of the performer.

Wu et al. (2009, 2011) measured the subjective valuation of reward in a movement based pointing task and also found that the subjective value function during these tasks were similar to those traditionally reported in financial decision making. O'Brien and Ahmed (2014) compared how subjective valuation of reward differed within an individual when they had to make reaching movements towards rewarded targets ($) while sitting and standing. Their results suggest that the subjective valuation of money in movement based decision making is similar to values commonly reported in economic tasks ($\alpha_{sit}$=0.52, $\alpha_{stand}$=0.68). In a follow-up study, they tested the generalizability of subjective valuation across movement types, specifically between standing, reaching and postural adjustments of the body center of mass (COM). The valuation parameter fits for reaching were $\alpha$=0.68 and for posture were $\alpha$=0.72 (O'Brien and Ahmed 2015). These results provide additional evidence that subjective valuation of reward is consistent between movement and traditional financial decisions.

*Models of temporal discounting:*

The value of a reward decreases the longer you have to wait. The rate at which time discounts reward (impulsivity) has been quantified predominantly through two

types of discounting functions, exponential (Hull 1943) and hyperbolic (Mazur 1987) (Figure 1.2). An exponential discounting function takes the form of:

$$V(t) = R \cdot \exp(-k \cdot t)$$ [ 1.3 ]

Where the value of the discounted reward, V(t), is based on the initial reward (r) being multiplied by the exponential where t represents the delay and k represents a rate of discounting with higher numbers signifying greater impulsivity. Identical parameters are involved in a hyperbolic function, however, this function makes slightly different predictions:

$$V(t) = \frac{R}{1 + k \cdot t}$$ [ 1.4 ]

Again, in this function, a higher value for k represents greater impulsivity. As predicted by both equations, an individual with a k of 0 has no temporal discounting and is indifferent to when they receive a reward.
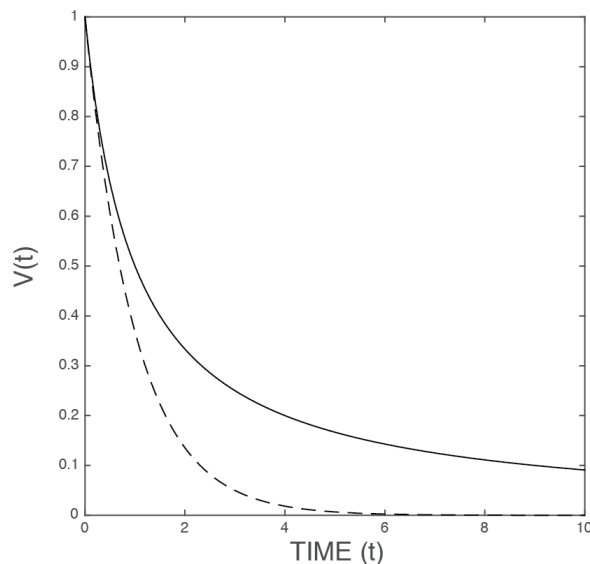


Figure 1.2 Temporal discounting of reward as predicted by hyperbolic (solid curve) and exponential (dashed curve) functions. Each curve predicts V(t) using an immediate value, R, of 1 and a discounting parameter, k, of 1.

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The following paragraphs compare how exponential and hyperbolic discounting functions can describe the level of impulsivity of an individual, and that this measurement can lead to predictions in both decision making and movement.

*Models of temporal discounting to predict decision making:*

As an individual becomes more impulsive, they are more likely to subjectively value immediate rewards much greater to similar rewards delivered later. By measuring an individual's level of impulsivity (k) we can make predictions for how long of a delay animals are willing to accept for a later reward. The justification of an exponential compared to hyperbolic discounting function to predict inter-temporal choice has been debated for decades (Mazur 1987; Green and Myerson 1996). In the next few paragraphs I will explain why hyperbolic over exponential models have been the preferred method of quantifying impulsivity in decision making.

Early experimental evidence pointing to a hyperbolic discounting function was presented by Mazur (1987). In his experiment, pigeons chose between receiving two seconds of access to food ($r_2$) or six seconds of access to food ($R_6$). The delay tied with $R_2$, ($d_2$), was fixed within a session and the delay with $R_6$ ($d_6$) was adjusted until pigeons were indifferent between the two rewards. This was repeated across session with different fixed delays, resulting in several indifference points between delays for $R_2$ and $R_6$. Throughout the experiment the reward magnitudes were held constant. As the delay for $r_2$ increased, the delay for $r_6$ increased linearly. The line from these observations was compared to the lines that were predicted by each candidate functions. These were

obtained by setting the discount function at each reward equal to each other and solving for $d_6$. Doing so for the exponential function resulted in the line:

$$d_6 = \frac{\ln(R_6) - \ln(R_2)}{k} + d_2 \qquad [\,1.5\,]$$

This equation predicts that the slope of the line should be 1, with an intercept that depends on the difference between the two rewards. For hyperbolic, the line was:

$$d_6 = \frac{R_6 - R_2}{R_2 \cdot k} + \frac{R_6}{R_2} \cdot d_2 \qquad [\,1.6\,]$$

This equation makes a prediction that distinguishes it from exponential in that as long as the rewards are not equal, the slope of the indifference line will be different from 1 (>1 if later reward is larger). Observed indifference slopes from the pigeons ranged from 2-3. When setting the discounting factor to 1, the hyperbolic function was able to account for > 90% of the variance in the choice data.

A hyperbolic discounting function can further be justified over an exponential function through its ability to predict a phenomenon referred to as reversals of preference (Rachlin and Green 1972). Reversal of preference describes an observation where preferences of inter-temporal-choice at one time point do not predict preferences when the same time differences between choices are framed at a later time point. For example, imagine you are given the option between receiving four dollars now or five dollars in a week. Lets assume that most people would choose the immediate four dollars. Now let us view these same choices, but with a further six-month delay added to both options. Any individual that would now prefer the five dollars delivered in 25 weeks over the alternative four dollars in 24 weeks have exhibited reversal of

preference. A function that can describe this reversal of preference must predict an intersection in value between delayed rewards at different global delays (Figure 1.3).
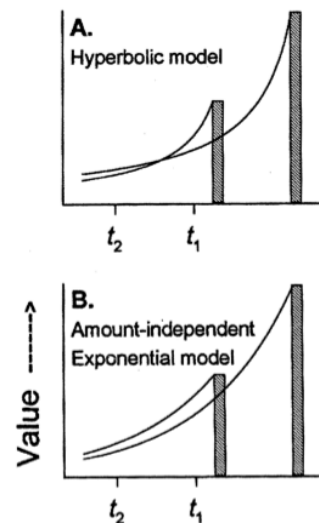


Figure 1.3 Reversal of preference is observed between larger and smaller rewards depending on at which point in time the decision is made. A hyperbolic model (A) shows a preference for the smaller reward at time $t_1$, but a preference for the larger reward at a later time $t_2$. An exponential function (B) predicts the smaller reward when asked at either time $t_1$ or $t_2$. Adapted from Green and Myerson (1996).

Rachlin and Green (1972) tested for the reversal of preference by having pigeons first make decisions which was followed by a delay (t). After the time t, the pigeon either immediately received 2 seconds of reward followed by a subsequent 6-second delay, or a 4-second delay followed by a subsequent 4 seconds of reward. With low t, pigeons preferred the smaller, earlier reward. As t increased, preferences switched to the higher, later reward, as predicted by a hyperbolic model. Similar switching behavior has been recorded in humans as well when making inter-temporal choices between different monetary rewards delivered over different universal delays (Kirby and Herrnstein 2016).

Adding time to a reward discounts the value of that reward with the rate of discounting depending on the level of impulsivity from the decider. There are several functions that can be used to describe this decay function, most commonly, exponential and hyperbolic (Hull 1943; Mazur 1987). The above examples suggest that hyperbolic discounting functions are best suited for measuring the effect of time on reward across a range of different decision making situations (Mazur 1987; Haith et al. 2012).

*Models of temporal discounting to predict movement*

Let us say that in the example at the beginning of this review you chose to go to the grocery store for dinner. At the store there are a pile of apples. Some apples are fresh and some are rather old and bruised. When you reach to inspect these apples, you will do so with a preferred speed and duration that is based on the expected utility of the movement. A model of utility that includes temporal discounting would predict that the optimal movement duration to reach for the more rewarding fresh apples would be faster than the less rewarding bruised apples because of their greater devaluation over time (Shadmehr 2010). This prediction has been tested experimentally to explain variation across movement preferences in humans and other animals.

Using a discount function to quantify temporal discounting of reward should allow us to make two predictions. First, increasing time will result in greater loss of value for an initial r. Second, increasing impulsivity will result in greater loss of value for a given r and t. Both humans and other animals make saccades faster to targets when that target is more rewarding (Takikawa et al. 2002; Xu-Wilson et al. 2009). In human children, naturalistic saccade velocity is much faster than mature adults (Fioravanti et al. 1995).

They also show much greater levels of impulsivity in temporal discounting paradigms (Green et al. 1999).

Models that have attempted to explain movement vigor have used both exponential (Rigoux and Guigon 2012) and hyperbolic (Shadmehr et al. 2010, 2016) functions of temporal discounting. To test the relative predictive power of the two functions, Haith et al. (2012) designed an experiment where participants made saccades of a fixed amplitude without changing reward. Their only manipulation was that they varied inter-trial-intervals (ITI), resulting in a drifting rate of reward. A hyperbolic function would predict that altering ITIs would alter the shape of the curve, while in an exponential would only alter the scaling (Figure 1.4).
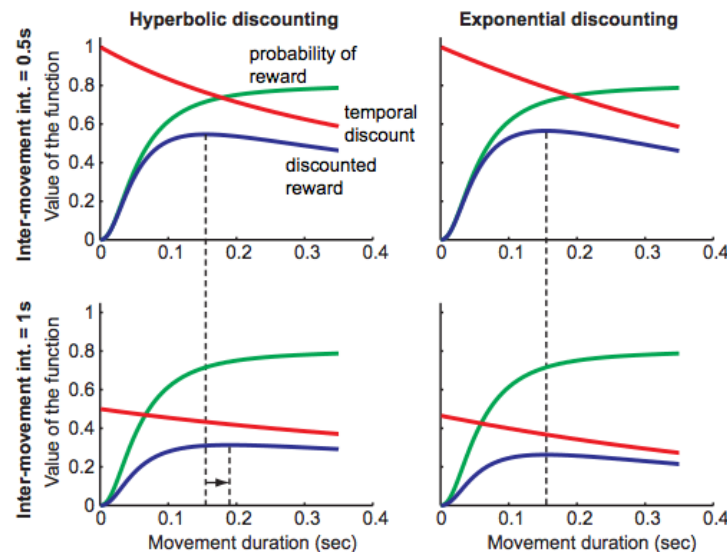


Figure 1.4 Model predictions for optimal saccade durations across different ITIs. Hyperbolic discounting predicts change in vigor observed when ITIs are changed. Adapted from Haith et al. (2012).

As ITI was shifted over the course of the experiment, saccade vigor responded as well, decreasing when ITI was lengthened and increasing when ITI was shortened. These

results strengthen the argument that time influences movement vigor by discounting reward. Modeling this discounting is most accurately captured by a hyperbolic function.

These observations provide evidence to suggest that time discounts reward hyperbolically. The ability for a single function to quantify temporal discounting in both decision making and movement preferences across species, age, and disease suggests the cost of time plays an important role in shaping utility.

*Models of effort*

Effort, like time, is a cost that discounts the value of a reward. As more effort is required before acquisition of a reward, the less valuable the reward becomes. There are several mathematical functions that have been proposed to describe the rate of discounting as effort costs increase. These models have been investigated almost exclusively in the realm of decision making. How effort is modeled in movement has mainly come from the field of optimal control. As this modeling was previously discussed in section 2, I will focus here on presenting evidence that effort discounting can be modeled either multiplicatively or additively in decision making.

*Hyperbolic models in decision making:*

It has been proposed that effort, like time, discounts reward hyperbolically where an initial reward (R) is divided by a denominator that is influenced by discounting parameter ($\beta$) [eq 1.3, k replaced with $\beta$ when referencing effort]. This model predicts that as the magnitude of effort increases, changes in valuation decrease (same predictions as in temporal discounting discussed in previous section). It also suggests

that higher rewards will be discounted at a faster rate than smaller rewards. Early studies investigating hyperbolic effort discounting were conducted by Mitchell (1999), where individuals exerted a full range of isometric grip force (10%-100% MVC) using a hand dynamometer. Participants then made decisions between generating MVC% for $10 or forgoing the effort for a smaller monetary reward. Fitting their discounting function using a hyperbolic model resulted in a discounting parameter of nearly zero (0.003). In a similar study by Prevost et al. (2010), participants (straight adult males) made decisions between exerting grip forces (15%-90% MVC) to view sexually explicit images for 3 seconds, or forgo the effort and view the same image for a shorter 1-second period. They also reported smaller changes in subjective value as effort increased, however exact parameter values were not reported. The limited results proposing that effort is discounted hyperbolically, provide surprisingly differing levels of discounting rates considering they were fitted using the same effortful task. Some studies that suggest hyperbolic discounting (Mitchell 1999) are justified on relatively weak evidence. They also fail to compare their results against linear and hyperbolic functions. While it appears that effort discounts reward, it is not justified to assume that it does so hyperbolically without modeling results with other potential models.

*Parabolic models*

Effort discounting using a parabolic function results in much different predictions from hyperbolic. In parabolic functions, effort is discounted additively rather than multiplicatively. These models make the prediction that as effort costs increase, their rate of reward discounts concavely, with greater changes in value occurring at higher

levels of effort. This hypothesis was motivated by the observation that the perception of force increases exponentially approximately to the power of 2 (Stevens and Mack 1959). Hartmann et al. (2013) were the first to probe a parametric discounting function such that effort discounted reward based on the function:

$$SV(effort) = R - k \cdot effort^2 \qquad\qquad [\,1.7\,]$$

Here the subjective value (SV) of the reward (r) is based on the level of effort squared which is further weighted by the discounting parameter k. Studies conducted by both Hartmann et al. (2013) and Klein-fugge et al. (2015, 2016) had participants choose between making isometric handgrip forces for higher monetary rewards or no forces for lower rewards. In both studies, the amount of effort tied to the reward influenced how participants made their decisions. Participants' choices were best explained by a parabolic model of effort where discrete changes in lower magnitudes of effort had little effect on reward, while changes at greater magnitudes resulted in steeper discounting of reward.

Compared to the exhaustive literature in modeling the subjective value of reward and temporal discounting of reward, relatively little research has been published on how effort discounts reward in the absence of a time interaction. Before a specific model of effort discounting is agreed upon, effort discounting of reward should be investigated using other effortful tasks such as reaching to probe whether other implicit costs such as accuracy or discomfort (especially at higher MVCs) could be influencing utility in this specific effortful task.

*Modeling interactions of reward, time, and effort*

Throughout this document I have presented how animals independently value different forms of reward as well as different forms of costs that are often required to acquire rewards. However, when behaving in a complex environment, these costs and rewards interact. In the following paragraphs I present models that describe how reward, time and effort interact to generate a utility that attempt to explain decision making and/or naturalistic movement preferences.

One of the most influential studies tying reward, effort, and time was conducted by Bautista et al. (2001). They trained starlings to either walk (low effort) or fly (high effort) a range of distances to obtain different quantities of food. They then measured the metabolic cost (effort x time) of the actions involved in obtaining the food (walking or flying) against the metabolic gain from the food reward to predict how starlings establish movement utility. They proposed three utility functions to predict preferences: maximizing gross rate of reward, minimizing gross metabolic cost of effort, and maximizing net metabolic rate (Figure 1.5). Their results found that starlings chose to walk or fly by optimizing the net metabolic rate over time (total calories gained minus total calories used moving divided by total time).
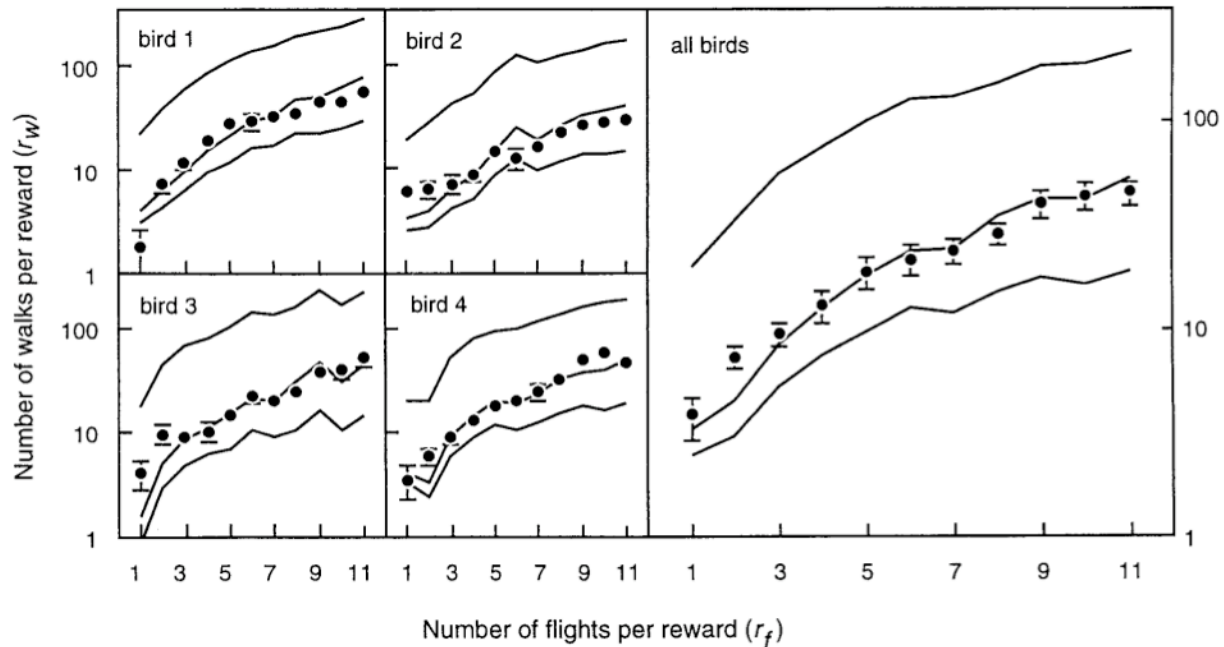
Figure 1.5 Results from Bautista et al. [2001]. Points represent preferred number of walks based on number of flights per reward. Upper line represents minimizing gross metabolic cost, middle line represents maximizing net metabolic rate, bottom line represents maximizing gross rate of reward. Net rate was the model that best fit observations. Adapted from Bautista et al. (2001).

The net energetic gain hypothesis has been supported in several other animal foraging studies as well. Shorebirds often have to choose between two types of major foraging methods. They can either peck for food at the surface (low effort, low reward), or probe for food by striking into the sediment (high effort, high return). As the penetrability of the sediment layer changes, so does the cost of probing. Kuwae et al. (2010) were able to measure metabolic intake rate for pecking and probing in environments with varying sediment penetrability and found that the preferred foraging method corresponded to maximizing net energy intake rate. When the sediment was easily penetrable, probing was preferred. As the penetrability became more difficult, net metabolic rate for probing decreased resulting in the birds switching to pecking. In another example, Dumont et al.

(1998) had sheep choose between immediate low calorie feed or an alternative high calorie feed that varied in quantity and distance from the animal. By calculating the energy gained from the high quality feed and the time spent walking to the good quality hay, they were able to predict at which combinations of quantity and distance the sheep would travel for the high quality food. Interestingly, a utility based on net energetic rate is based entirely on objective measurements of time, energy, and reward. While this is advantageous in that it is based on objective measures, they fail to consider the subjective valuations of such costs. This is especially surprising, given that starlings exhibit hyperbolic temporal discounting (Shapiro et al. 2008).

As we improve our understanding of how animals subjectively value reward, time, and effort, new models of utility have begun to emerge that are able to make accurate predictions both in movement and decision making by considering subjective valuations of rewards and costs.

Rigoux and Guigon (2012) were the first to propose a universal model of utility that can explain decision making and movement. They developed an optimal control model based on a cost function including reward, time and effort. Parameters included a reward value for arriving at the end state, scaling factors for reward and effort (free parameters fit to capture vigor), and a temporal discounting factor that exponentially discounted both reward and effort. They used a data set by Stevens et al. (2005) where two species of monkeys exhibited different decision making preferences between walking a short distance to small rewards and a longer distance to large rewards. Using movement durations measured during forced trials for each distance, they fit the 'vigor' parameter and found that a difference in vigor parameter values could explain the

difference in choice between species for the near/small reward vs the far/large reward. These results provided the first evidence that information from naturalistic movement behavior could be used to explain decision making preferences. However, effort was not measured, but rather represented abstractly as the sum of squared estimated forces.

A more recent model proposed by Shadmehr et al. (2016) goes a step further by representing effort based on the changes in metabolic cost of a movement (an empirically based function of time, distance and mass). This model uses a hyperbolic discounting function rather than exponential because of its improved performance in explaining discounting in the presence of altering inter-trial-intervals, something an exponential model fails to capture (2012). Additively combining discounted reward and effort results in a utility function with a peak utility corresponding to optimal duration (Figure 1.6).
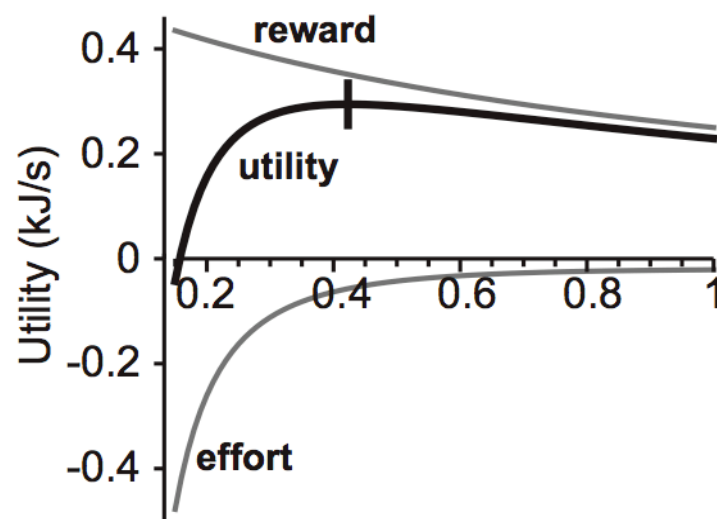


Figure 1.6 Utility function establishing optimal movement duration (x axis) based on reward and effort, both discounted by time. Adapted from Shadmehr et al. (2016).

The model's ability to explain decision and movement utility across a range behaviors in different animals provides support for the idea that the brain represents effort as metabolic cost. It can successfully explain preferences for reach direction (Wang and Dounskaia 2012) as well as differences in vigor due to effective mass (Gordon et al. 1994), recreate foraging strategies in starlings (Bautista et al. 2001), and preferences in producing forces of differing magnitude and time (Kording et al. 2004). This framework suggests that a utility in which effort is represented objectively as metabolic cost, and both effort and reward are discounted hyperbolically by time, can explain both decisions and movements across a range of animals and behaviors. However, work still remains to test performance across populations that differ in their subjective valuation of reward, effort and time.

In this last section, I have presented an overview of how reward, time, and effort can be combined to explain preferences in both decision making and movement. For a model of utility to have power across different species, ages, and disease, it is important to consider how these variables can be subjectively valued. Observations of the subjective valuation in reward, time and effort have been well recorded independently, but they are only now beginning to be combined to model behavior in a range of complex environments.

# CHAPTER 2

# THESIS OBJECTIVES

## 2.1 Motivation

The value of our environment is constantly changing, with these changes being reflected in how an animal adapts its behavior. While environmental costs and rewards have been used to explain a range of movement behaviors in many animal species, there is surprisingly little data in regards to whether these same variables can explain movement preferences in humans. This current collection of work aims to explore how effort, time, and reward contribute towards establishing a utility for each prospective movement and how differences in the valuation of these variables may explain movement preferences both within and across healthy human populations. By combining value functions developed in economics with an ecological based currency, I attempt to explain an individual's preferences across decision making and movement. A better understanding of these behavioral interactions between reward, time, and effort can hopefully lead to improvements in methods used for explaining and improving movement preferences observed across humans of different age and disease.

## 2.2 Specific Aims

In this dissertation I explore how interactions of effort, time, and reward interact to collectively explain preferences when selecting both *between* alternative movements and when establishing the vigor *within* individual movements. The specifics of this endeavor are addressed in the following aims:

AIM 1: Determine how effort, quantified as a physiologically based metabolic currency, is valued when choosing between different risky movements decisions.

AIM 2: Establish how individuals consider conflicting effort and temporal costs when selecting between walking and running gaits of varying distances.

AIM 3: Examine how reward discounts the cost of effort when selecting vigor in unconstrained reaching movements.

AIM 4: Examine whether healthy aging alters the interactions between costs and benefits when selecting vigor in unconstrained reaching movements.

## 2.3 Outline

For the remainder of this thesis (chapters 3-7) I present a collection of four experiments and conclude with a short description of their collective implications.

Chapter 3 presents an experiment adapted from a classic decision-making paradigm based on cumulative prospect theory. In this experiment I explored whether individuals subjectively value increasing effort in a simple reaching task and if this subjective distortion was consistent across the group.

Chapter 4 presents an experiment probing how participant-specific weightings of effort and time explain gait decisions between walking and running. I then attempt to explain

how representations of these competing costs explain differences in self-selected gait speeds both within and across subjects.

Chapter 5 presents an experiment exploring how young adults adjust the vigor of their movements in response to a changing reward landscape. In this specific environment, neither the quality nor quantity of reward was contingent on any aspect of vigor.

Chapter 6 consists of two experiments. In the first experiment, I measured how older adults adjusted vigor in response to changing reward. In the second experiment I measured the metabolic cost of reaching in older and young adults to probe whether reward sensitivity between age groups could be explained as a results of changes in the representation of effort, reward or both.

Chapter 7, the final chapter of this thesis, summarizes the main findings of the presented work and discusses their broader implications.

## 2.4 Significance

The following series of projects introduce a diverse range of datasets with the results from these datasets collectively describing how costs and benefits interact to establish a utility for each of our actions. These experiments were developed to help advance our understanding of the exciting relationship between movement and decision making. The specific advancements of this dissertation include the first example of how humans value increasing effort in reaching when quantified in a physiological framework, how this same cost of effort interacts with time to explain variability in a different set of movements: gait, how increased reward discounts effort when selecting movement

vigor in reaching, and how the representation of these reward and effort variables change with healthy aging. These experiments provide a range of examples where representing the cost of effort as a metabolic cost can accurately capture how humans establish preferences both between movements and within movements. Movement is a fundamental component essential for a healthy life. These results have implications for improving our understanding of why certain neurological diseases cause individuals to adapt pathological movement patterns and how different incentive structures may potentially be used to reinforce healthy movement patterns and improve an individual's overall quality of life.

# CHAPTER 3

# USING METABOLIC COST TO QUANTIFY THE SUBJECTIVE VALUE OF PHYSICAL EFFORT

## 3.1 Abstract

Economists have known for centuries that to understand an individual's decisions, we must consider not only the objective value of the goal at stake, but its subjective value as well. However, achieving that goal requires expenditure of effort. Surprisingly, despite the ubiquitous role of effort in decision making, we currently do not understand how an individual subjectively values effort in daily movements. Part of the difficulty arises from the lack of an objective measure of effort. Here I used a physiological approach to address this gap in our knowledge. I quantified objective effort costs by measuring metabolic cost via expired gas analysis as participants performed a reaching task against increasing amounts of resistance. I then used neuroeconomic methods to quantify each individual's subjective valuation of effort. Rather than the diminishing sensitivity observed in reward valuation, effort distortions were idiosyncratic. An equal number of participants exhibited increased sensitivity and decreased sensitivity to effort, leading to an objective valuation of effort on average. This is significantly less than the increasing, near-quadratic sensitivity to effort observed previously in force-based motor tasks. Moreover, I found that a utility in which effort discounting was additive, rather than hyperbolic, explained participant's effort based decisions. Together, these findings demonstrate that in contrast to monetary decisions in which subjective value exhibits diminishing marginal returns, effort costs are valued more objectively in low effort, reaching movements that are common in daily life.

## 3.2 Introduction

Economists have known for centuries that to understand an individual's decisions, we must consider not only the objective value of the rewards at stake, but their subjective value as well (Bernoulli 1954; Tversky and Kahneman 1992). There exists a nonlinear relationship between objective rewards and their subjective value whereby individuals often value each additional increment of objective reward with diminishing subjective value (i.e. diminishing sensitivity). Understanding such nonlinearities has proven critical to our ability to explain decision making across a range of economic environments and domains. However, every reward ultimately requires an action to obtain it, and that action inevitably requires effort. Effort is an inherent cost to many, if not all decisions, but we have yet to understand its role in decision making. This is surprising given that many neural disorders involve a form of movement deficiency. In Parkinson's Disease, for example, the cardinal symptom is bradykinesia, or slowness of movements. The disease arises from a loss of dopaminergic neurons in the substantia nigra. While dopamine is generally thought to modulate reward signals, there is increasing evidence for its role in determining how hard humans and other animals will work for a given reward (Salamone et al. 1991a, 1994a; Phillips et al. 2007; Treadway et al. 2012). This implicates an exaggerated sensitivity in valuation of effort as one of the possible underlying mechanisms of movement slowing in Parkinson's Disease (Mazzoni et al. 2007).

One of the main obstacles to this line of research is the lack of an objective measure of effort costs. Psychophysical measurements demonstrate that the perception of effort increases nearly quadratically with increases in effort (Stevens and Mack

1959), suggesting that effort is valued in a similar manner. However, these studies, as well as previous attempts to understand how effort discounts reward in decision making, have used proxies for effort such as isometric force production (Kording et al. 2004; Schmidt et al. 2008a, 2012; Prévost et al. 2010; Hartmann et al. 2013; Kurniawan et al. 2013; Klein-Flügge et al. 2015), estimated force production (Morel et al. 2017), number of targets acquired (Croxson et al. 2009) and button presses (Venugopalan et al. 2011; Treadway et al. 2012). So we do not know if the objective effort costs were accurately represented by these experimental manipulations of effort. Some also required near maximum levels of exertion which may have led to additional costs such as pain, discomfort or fatigue. Others have provided choices coupled with monetary rewards without accounting for the accompanying nonlinearity in that reward's subjective value function (Schmidt et al. 2008a, 2012; Croxson et al. 2009; Treadway et al. 2012; Hartmann et al. 2013; Kurniawan et al. 2013). I present a paradigm to circumvent these issues by examining low-effort movements that are representative of the everyday movements we make, controlling for reward, and critically, measuring objective effort directly in the form of metabolic cost.

Our understanding of movement control has a long history of implicating effort as an underlying determinant of preferred movement characteristics. In locomotion, effort costs, represented objectively as metabolic costs, have been used to predict preferred walking speed, step length, step width, and arm swing in healthy individuals (Ralston 1958; Zarrugh et al. 1974; Arellano and Kram 2011; Selinger et al. 2015). When represented as metabolic cost, effort-informed decision-making in reaching can account for both the choice of action as well as the kinematics of the ensuing movements

(Shadmehr et al. 2016). Metabolic costs are also used to explain foraging decisions in a range of animals (Charnov 1976; Richardson and Verbeek 1986; Bautista et al. 2001; Stevens et al. 2005). Both the breadth and history of this literature provide a strong rationale to propose metabolic cost as an objective measure of effort.

Effort costs are also a cornerstone of optimal control models of movement control, which are capable of explaining observed movement trajectories across a range of conditions (Todorov and Jordan 2002; Izawa et al. 2008; Qian et al. 2012). Such models invariably assume that the objective cost and the subjective valuation of the cost are one and the same. However, there is strong evidence that the subjective valuation of movement-related costs such as time and probability differ from their objective values (Mazur 1987; Tversky and Kahneman 1992). When considering the subjective value of these costs, models of movement control can better predict movement-related behaviors (Wu et al. 2009; Shadmehr 2010; O'Brien and Ahmed 2015).

Here I will address two main questions regarding how physical effort costs are considered for effort-based decisions in healthy adults. First, is there a nonlinear relationship between the objective physical effort cost, quantified as metabolic cost, and its subjective value? Second, how does effort discount decisions? Together, these findings will help advance our understanding of the role of effort in both decision making and movement.

## 3.3 Methods

*Participants*

Twenty participants were enrolled in this experiment (25±4 years, 72.90±9.21 kg, 7F, 13M). Each participant gave written informed consent as approved by the University

of Colorado Institutional Review Board and received $10/hour for participating. All participants completed a training session, metabolic session, and one choice behavior session. Thirteen repeated a second choice behavior session. Each session took place on different days.

*Training session*

The purpose of the initial session was to familiarize participants with reaching against a resistive force as well as to train them to reach under a constrained time limit. The task consisted of making 20cm out-then-back reaching movements between a home circle and a rectangular target (15cm wide) (Figure 3.1A, without gauge). Visual feedback was provided at the end of each movement to ensure that movement duration fell between 550ms and 650ms. If the cursor arrived within the desired duration, the target flashed yellow and made a pleasant beep. If the cursor arrived too early, the target turned green with no audio stimulus and if the cursor arrived too late, the target turned gray with no audio stimulus. This feedback was necessary to promote a consistent velocity profile. Consistent reaching kinematics were necessary because throughout the reach, participants experienced resistive forces that depended on the velocity of the cursor. Velocity dependent forces were generated according to the following equation: $[F_x \ F_y] = -b[V_x \ V_y]$, where $F_x$ and $F_y$ represent horizontal and vertical forces, $V_x$ and $V_y$ the corresponding handle velocities, and b is a constant describing the gain on the resistance. There were five conditions: b= 0 (no forces), 30, 45, 60 and 70 Ns/m, each presented in blocks of 50 trials in randomized order.

Immediately following each block, participants reported a modified Rating of Perceived Exertion (RPE, (Borg 1970) where they were asked to rate the physical effort

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required to complete the task at each resistance gain. The possible scores ranged between 6 (low effort) and 20 (high effort). The first block tested was 0 N•s/m followed by the second block tested at 70 N•s/m. For these first two blocks, participants were directly informed that they were the easiest and hardest conditions. By providing these two blocks early, participants were able to set a floor and ceiling score to base the remaining three conditions within. RPE scores did not represent absolute levels of exertion, but instead levels of exertion relative to an already experienced maximum (70N•s/m) and minimum (0Ns/m) resistance. After each block participants completed 20 washout trials against no resistance (0 N•s/m). Each resistance condition (sin null resistance) was repeated three times for a total of 13 blocks. The last block of each condition was inspected to confirm that the increase in resistance gain reflected a relative increase in RPE score.



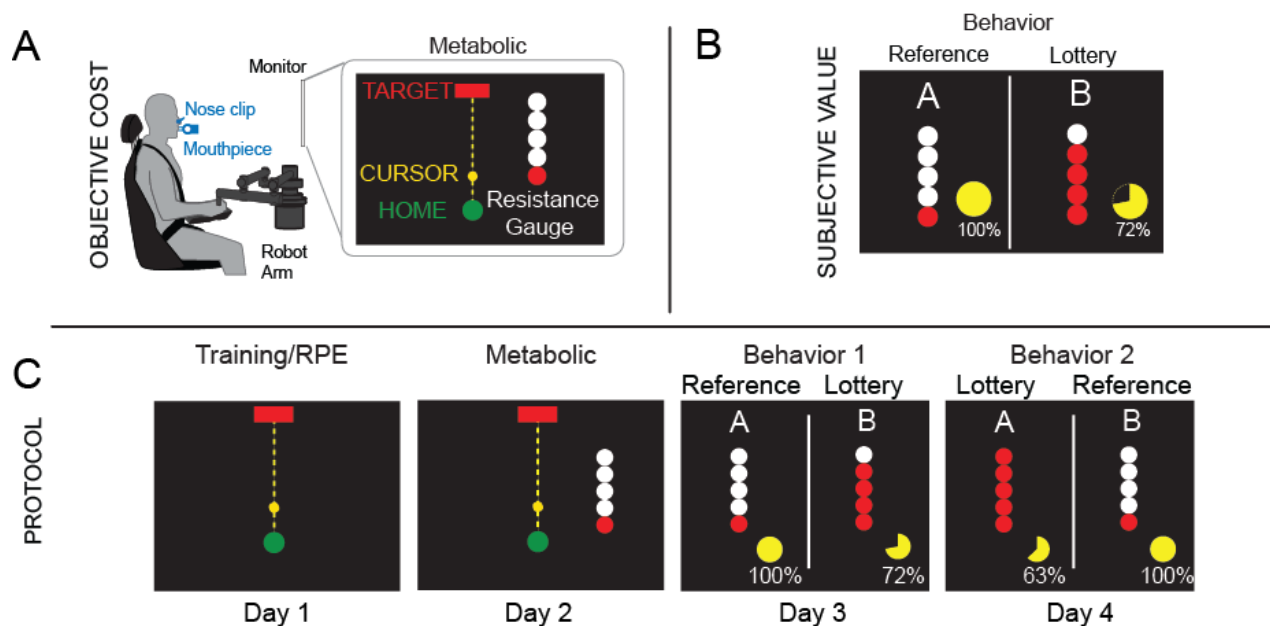Figure 3.1 Experimental Design. *(A)* Objective Cost. Participants moved a cursor out and back against a resistive force field. While reaching they wore a nose clip and breathed through a mouthpiece that measured rates of oxygen consumption and carbon dioxide production. The gain of the force field was disclosed to the participant through the use of a resistance gauge that ranged from 1-5 dots with increasing red dots

corresponding to increasing resistances. *(B)* Subjective Value. Subjective valuation was calculated based on decision making behavior in this session. Participants made decisions between reference and lottery options based on which option required the least amount of effort. The reference remained constant throughout all trials and represented a sure bet (100%) of reaching against the lowest resistance (1 dot). The lottery option was a combination of different resistance and probability pairs. The consequence of each decision was the risk of performing 5 minutes of reaching at the displayed resistance with the alternative outcome being to sit quietly. *(C)* Protocol. In the training/RPE participants made velocity constrained reaches against undisclosed resistance between a home circle (green) and a target (red) and reported the relative exertion on a scale from 6 (low) to 20 (high). In the metabolic session, participants reached against known resistances and learned to associate the resistance gauge with the experienced resistance. In behavior sessions 1 and 2, participants were instructed to decide which option (reference or lottery) required the least amount of effort.

*Metabolic session*

In the metabolic session, the objective effort cost (i.e. metabolic cost) of reaching against resistance was measured using methods previously developed by others in my laboratory (Huang et al. 2012; Huang and Ahmed 2013, 2014; Shadmehr et al. 2016). Upon arrival at the laboratory, participants completed three 6-minute baseline blocks where they sat quietly and I measured their metabolic rate. This was followed by trial blocks of reaching against resistances of 0, 30, 45, 60, and 70 Ns/m. The resistance in each block was fixed, but the order of blocks was randomized. Each reaching block consisted of 300 trials lasting ~7 minutes. During each block, a number of dots were displayed on the side of the monitor corresponding to the magnitude of the force field gain (Figure 3.1C, 1 dot=lowest gain, 5 dots=highest). Participants were instructed to associate the dots with the force field they were experiencing. These dots were used in the upcoming behavior session to represent effort levels. Between each reaching block the participant rested for 5 minutes.

Expired gas analysis was used to calculate the net normalized metabolic cost (J/kg) of seated resting and of seated reaching against resistance. Participants wore a nose-clip and breathed into a mouthpiece during all baseline and reaching blocks. A metabolic cart (ParvoMedics, TrueMax2400) was used to sample the amount of consumed oxygen (O2, l/min) and expired carbon dioxide (CO2, l/min) over 5 second intervals. At the beginning of each metabolic session, gas fractions were calibrated using a certified standard gas mixture and flow rate was calibrated using a 3-liter syringe under various flow rates. Respiratory exchange ratio (RER) ($CO_2/O_2$) was monitored to confirm that each subject was within physiological ranges of aerobic respiration (0.7-1.0). Using the average $O_2$ and $CO_2$ for the last 3 minutes of each reaching condition, gross metabolic power (J/s) was calculated using the Brockway equation (Brockway 1987). Net metabolic power for each condition was calculated by subtracting the lowest average gross power of the three baseline blocks from the average gross metabolic power of that condition. Net metabolic power measured for each resistance was multiplied by the duration of the activity to represent the net *metabolic cost* of reaching against that resistance (J). I refer to the net metabolic cost of reaching as the objective effort cost.

*Behavior Session 1 & 2*

In the behavior sessions, participants made choices between risky effort lotteries. Each choice consisted of a reference option and a lottery option (Figure 3.1B). The reference option represented a sure bet (100% chance) of having to reach for five minutes at the lowest resistance. The reference option was unchanged across all trials

and always available as an option. The alternative option was the lottery. The consequences of the lottery option consisted of either a displayed probability of performing a high-effort reach versus the alternative outcome of sitting quietly for five minutes. I varied the value of the lottery using combinations of one of the five resistances alongside one of five probabilities (53%, 63%, 72%, 84%, 95%), for a total of 25 lottery combinations, which were repeated 6 times for a total of 150 trials. At the end of the behavior session, the participants' choices were realized by performing the results of three randomly chosen choice trials. If the subject chose the reference option, then they performed five minutes of reaching against zero resistance. If the participant chose the lottery option, they rolled two 10-sided dice where one die represented the 10s placeholder and the other the 1s placeholder. A pair of 10s represented rolling a 100%. If the number rolled was higher than the percentage of the chosen lottery, the participant would sit in the chair for five minutes and not have to perform the reaching task. Otherwise, they performed five minutes of reaching against the resistance assigned to the lottery.

Thirteen participants returned for a second behavioral session to test for consistency in decision-making strategies across days. Procedures during the second behavior session were nearly identical to the first with the only differences being that the order of the 150 choices were re-randomized and the locations of the reference and lottery options were switched on the screen. To compare parameter fits across days I plotted an individual's day 1 fits against their day 2 fits. I then fit a simple linear regression across participants and compared that slope to unity.

*Quantifying Subjective Valuation and Probability Weighting:*

The metabolic cost (objective effort cost) measured across participants in the metabolic session was combined with individual choice behavior in the behavior session to calculate each participant's specific utility function for effort. Their choices were used to fit decision making parameters found in utility functions derived from Cumulative Prospect Theory (Tversky and Kahneman 1992) using maximum likelihood estimation. I describe the expected utility of each decision according to the interactions of effort and probability. I represent the subjective value of effort according to the function:

$$SV(x) = R - x^{\varepsilon} \qquad\qquad [\,3.1\,]$$

where *R* is the pre-discounted reward value of the option which is assumed to be constant between lottery and reference options. The cost of effort is represented as x and is the net metabolic cost of reaching for 5 minutes (the duration of the choice realization) when compared to sitting quietly. This cost is subjectively valued as described by $\varepsilon$, with values of $\varepsilon > 1$ meaning that sensitivity to effort grows with increasing objective effort.

I represent the effects of probability for each decision according to the probability weighting function:

$$\omega(p(x)) = \exp[-(-\ln(p(x))^{\gamma}] \qquad\qquad [\,3.2\,]$$

Here, *p*(x) represents the probability of accruing the effort cost, x, and the weighting of this probability is defined by the variable $\gamma$. When $\gamma < 1$, low probabilities are overweighted and high probabilities are underweighted. The opposite is true when $\gamma > 1$, low probabilities are underweighted and high probabilities are overweighted. In the current protocol, I only tested probabilities above the inflection point of the curve.

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I described the overall expected utility (E[U]) of each reference and lottery option based on the contributions of their subjective value and weighted probability, defined as:

$$E[U] = SV(x) \cdot \omega(p(x))$$ [ 3.3 ]

The values for $\varepsilon$ and $\gamma$ were both fit according to the observed probability of choosing the lottery ($P_L$) as described by the logistic function:

$$P_L = \frac{1}{1 + e^{k(E[U_L] - E[U_R])}}$$ [ 3.4 ]

In this equation the variable $k$ is another free parameter used to describe the slope of the logistic curve. All three free parameters $\varepsilon$, $\gamma$, and $k$, were fit using maximum likelihood estimation.

*Alternative models*

In addition to the full three-parameter model described above, $M_{full}$, I also tested three additional models of decision-making. First I compared the performance of the full model to a two-parameter model where effort was valued objectively, i.e. it increased linearly with metabolic cost ($M_{lin}$, $\varepsilon=1$) with γ and $k$ being free parameters. The second alternative model was two-parameter model where effort was subjectively valued quadratically, ($M_{quad}$, $\varepsilon=2$). This function implies that effort is consistently subjectively valued quadratically, meaning that small increases in effort are valued as less costly compared to larger increases in effort. This model also included γ and $k$ as free parameters. Lastly, I considered a hyperbolic effort discount function in which reward was discounted hyperbolically by effort, $M_{hb}$. Here the subjective value of the option is represented as:

$$SV(x) = \frac{R}{1 + x^{\varepsilon}}$$ [ 3.5 ]

In a hyperbolic function, we include $R$ as an additional free parameter because it does not cancel when comparing utilities of options with reward of equal magnitude, as in equation 3.1.

*Statistics:*

The effect of resistance on metabolic cost, RPE, and frequency of choosing the lottery (both observed and model) were quantified using a simple linear regression model. The parameters $\varepsilon$ and $\gamma$ were compared to unity using independent t-tests.

Comparing the observed frequency of choosing the lottery to the model frequency of choosing the lottery was performed with a linear mixed effects model in both effort and probability comparisons. In these comparisons, a dummy variable was used to indicate whether behavior was observed or modeled. The analysis of the effect of resistance on reaching velocity and target deviation was performed with a repeated measures analysis of variance. All statistical analyses were conducted using a significance level of $\alpha=0.05$. Unless otherwise noted, descriptive statistics are explained as mean [95% confidence interval].

Goodness of fit of the full additive model which considered subjective value, $M_{sv}$, was compared to the alternative models, $M_x$, using Bayes factors (BF):

$$BF = \frac{P(M_{sv}|D)}{P(M_*|D)} = \frac{P(D|M_{sv})P(M_{sv})}{P(D|M_*)P(M_*)}$$ [ 3.6 ]

Bayes factors were approximated with the Bayesian Information Criterion (BIC, Schwarz 1978), calculated as the log likelihood of the model with the best fit parameters, minus a penalty for the number of parameters, *n*, and datapoints, *m*:

$$BIC = \log\left(P\left(D|M,\hat{\theta}_M\right)\right) - \frac{n}{2}\log m \approx \log\left(P\left(D|M\right)\right)$$ [ 3.7 ]

BICs and Bayes factors were calculated for each subject, each model, and each model comparison. Aggregate BICs are presented as well as population-based Bayes factors, which were interpreted as p-values with the following adjustment: p=1/*BF* (Kass and Raftery 1995). Finally, I also present the protected exceedence probabilities (pxp) (CITE) using the spm_BMS function available in SPM12 software (Wellcome Trust Centre for Neuroimaging, London, UK; http://www.fil.ion.ucl.ac.uk/spm).

## 3.4 Results

I measured how metabolic cost changed as participants performed out-then-back reaching movements against a range of submaximal resistive forces. Participants then made a series of decisions between a sure-bet of having to perform low effort reaches (reference option) or risk performing higher effort reaches (lottery option). Using the metabolic cost of reaching as a physiologically based representation of objective effort, I then used cumulative prospect theory to quantify each individual's subjective valuation of effort. Most participants demonstrated a significant distortion between objective and subjective effort. In contrast to the diminishing sensitivity observed in financial reward valuation (Kahneman and Tversky 1979; Tversky and Kahneman 1992), effort distortions were idiosyncratic. An equal number of participants exhibited increased

sensitivity and decreased sensitivity to effort, leading to an objective valuation of effort on average across the group.

*Metabolic cost of reaching increases as a result of changing resistance*

Participants made 20cm reaching movements against 5 different velocity dependent force fields ranging in resistance between 0 and 70 N•s/m. As resistance increased, metabolic cost exhibited a significant, linear increase (Figure 3.2A, β= 98.54, R=0.70, p<0.001). To confirm that individuals perceived the differences in effort across conditions, I measured reported RPE for each resistance. The range of this scale was modified to reflect solely reaching behavior. There was a significant increase in RPE that correlated with an increase in resistance (Figure 3.2B, β=0.109, $R^2$=0.59, p<0.001). These results indicate that my measurement of effort was sensitive enough to quantify differences in effort conditions and also that these changes were perceivable by each participant.
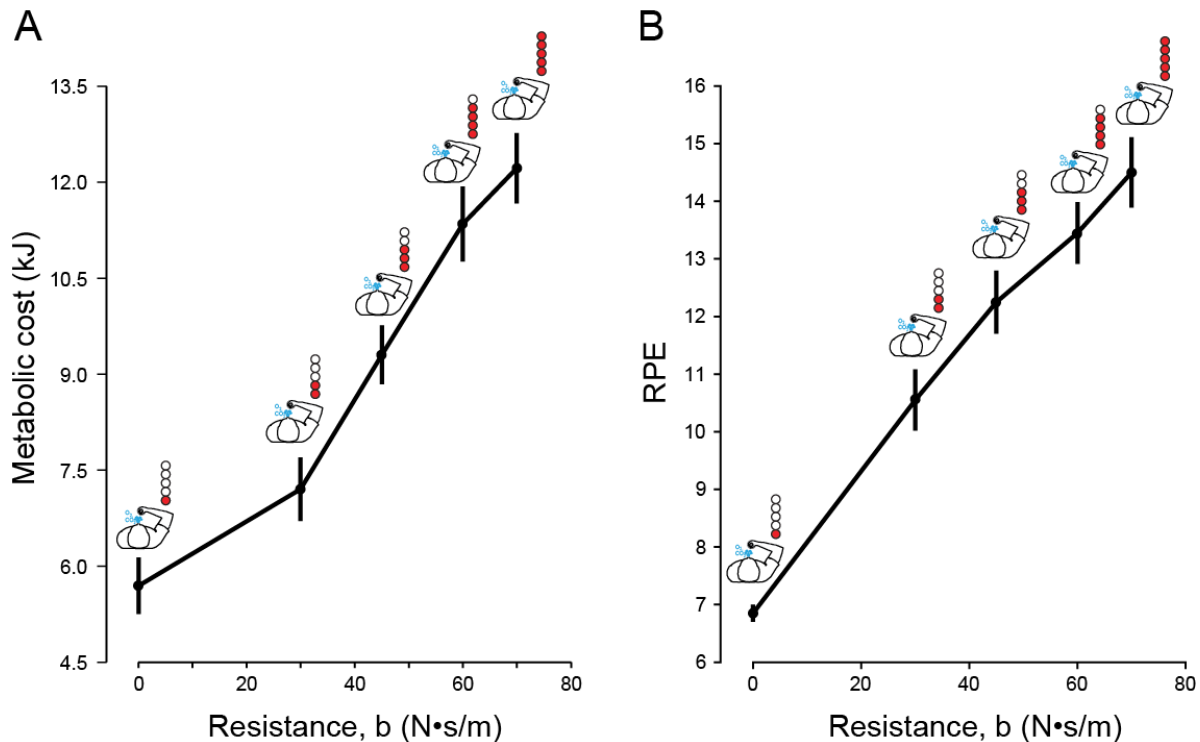
Figure 3.2 Effects of resistive force field on objective effort and rating of perceived exertion. A) Metabolic cost (objective effort cost) increases with increasing resistance. Metabolic costs were measured at resistances of 0, 30, 45, 60, and 70 Ns/m. Data points shown are the average across participants at each resistance. B) Rating of perceived exertion increases with increasing resistance. Scores based on relative exertion to other experienced resistances. Black bars represent 95% CI.

*Decision-making preferences were influenced by changing effort and probability*

Participants made choices between performing one of two reaching movements: a reference option and a lottery option. The reference option consisted of a 100% probability of performing a low-effort reach for five minutes. The lottery option consisted of either a known probability of performing five minutes of a high- effort reach versus the alternative outcome of sitting quietly for five minutes. I varied the value of the lottery's probability and effort levels using combinations of one of the five resistances and one of five probabilities. As the level of effort and/or probability increased in the lottery option, participants were more likely to choose the reference option (*Effort*: Figure 3.3C solid

lines, β=0.00013, *Probability*: Figure 3.3D solid lines, β=1.19, p's<0.001). These results provide evidence that participants were considering both the effort associated with the lottery option and the probability of performing the effortful reach when establishing preferences between the reference and lottery options.
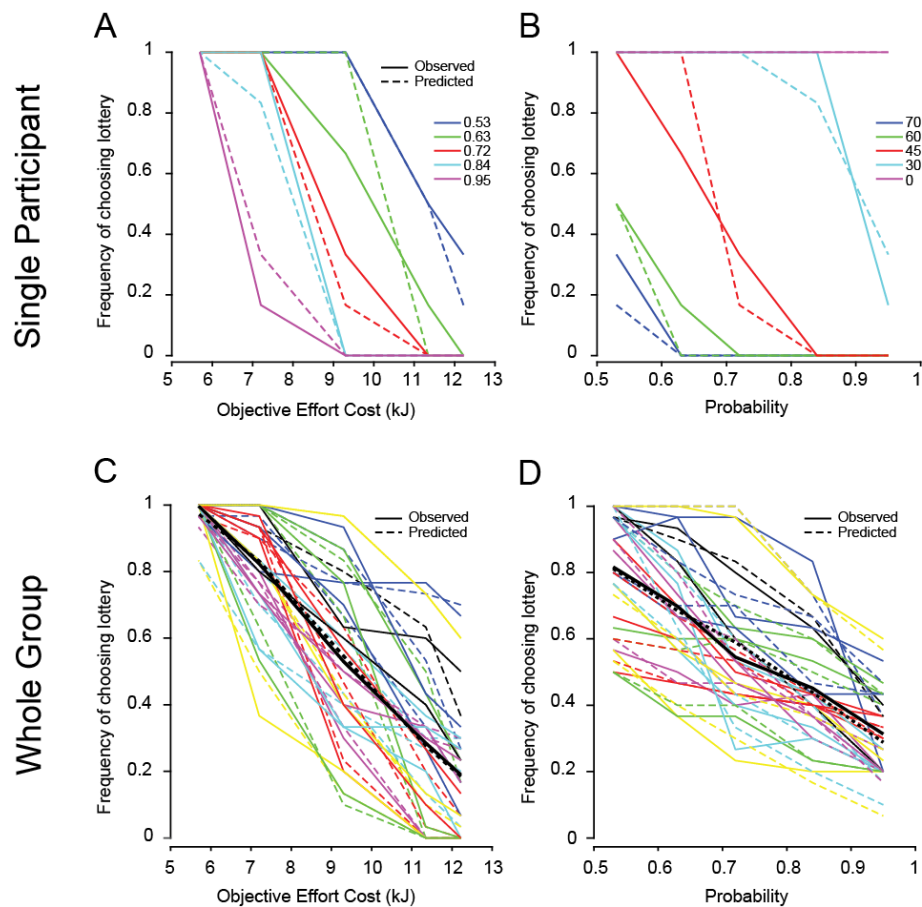


Figure 3.3 Observed choice behavior and full model predictions. A) Observed frequency of choosing lottery (solid lines) and full CPT model predictions (dashed lines) of a representative participant as a result of increasing objective effort cost across each tested probability. B) Observed frequency of choosing lottery and full CPT model predictions of same participant as a result of increasing probability across each effort level. C) Observed choice behavior and CPT model predictions of all participants as a result of increasing effort across all probabilities. Each thin colored line represents a different participant. Thick black lines represent average of whole group. D) Observed choice behavior and CPT model predictions of all participants as a result of increasing probability across all effort levels.

*Effort subjectively valued when making movement-based decisions*

I fit the free parameter $\varepsilon$, to explain how the frequency of choosing the lottery option was explained as a result of increasing effort. Values of $\varepsilon$ >1 represent a subjective overvaluation of effort where each additional increment of effort is valued with increasing sensitivity. Accordingly, $\varepsilon$ <1 represent a subjective undervaluation of effort where each additional increment is valued with decreasing sensitivity. An $\varepsilon$ =1 indicates an objective valuation of effort. Fitting a separate $\varepsilon$ for each individual, I found that participants exhibited idiosyncratic distortions in effort with approximately an equal number either over-valuing or under-valuing effort. Notably, there was no correlation between an individual's effort sensitivity and their specific net metabolic cost of performing the task (R=-0.0017, p=0.995). Across all participants the mean $\varepsilon$ was 1.04 [0.87 1.2] (mean [95% CI]) and was no different than 1 (p=0.650). This suggests that as a group there was no consistent bias in the subjective valuation of effort costs required to complete the reaching task. On an individual basis, I found that 10 out of the 20 subjects overvalued effort (Figure 3.4A, red lines) and the remaining 10 undervalued effort (Figure 3.4A, green lines).
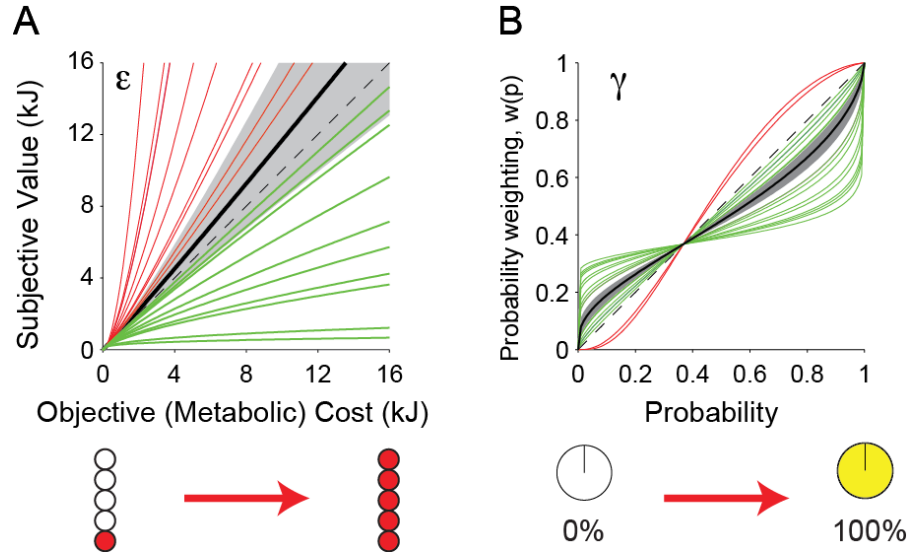
Figure 3.4 Full CPT model parameter fits. A) Subjective value ($\varepsilon$) for each participant (thin lines) and group (thick black line). B) Probability weighting ($\gamma$) of each participant and the whole group. Red lines represent parameters values >1 and green lines for values <1. Solid black line and gray shade represents mean and SEM across all participants. Dashed black lines represent lines of unity ($\varepsilon$, $\gamma$=1).

*Model including a subjective value of effort outperforms alternative value functions*

To determine the significance of the subjective value of effort, I compared the full three-parameter CPT model that considered each participant's fitted $\varepsilon$ and $\gamma$ parameters to a two-parameter model that exhibited no effort distortion ($M_{lin}$, $\varepsilon = 1$), a two-parameter model that exhibited a fixed quadratic distortion ($M_{quad}$, $\varepsilon = 2$), and a hyperbolic discounting function. I found that the full three-parameter model considering variation in subjective valuation and probability weighting performed significantly better than a model considering solely distortions in probability and an objective valuation of effort ($BIC_{sv}$=-632, $BIC_{lin}$=-365; $p<0.001$, Bayes Factor; $pxp_{full} = 0.985$, $pxp_{lin} = 0.015$). On an individual basis, I found that 13 of the 20 subjects exhibited distortions in that a full

model performed better than a reduced model without distortions ($BIC_{sv}>BIC_{lin}$). Of these 13, 8 overvalued effort and the remaining 5 undervalued effort.

I next compared the full model to a model considering a quadratic subjective valuation of effort. In contrast to $M_{sv}$ and $M_{lin}$, squaring the effort cost represents an overvaluation of effort that is consistent across individuals. I found that the model considering subjective valuation and probability weighting performed significantly better than a model considering solely distortions in probability ($BIC_2=-1311$; $p<0.001$, Bayes Factor; $pxp_2=0.0001$). On an individual basis, 15 of the 20 subjects exhibited distortions in that a full model performed better than a reduced model without distortions ($BIC_{sv}>BIC_2$).

Lastly, I compared the full model which considers reward and effort additively, to a hyperbolic discounting model. However, the hyperbolic model significantly underperformed the model in which utility is the sum of reward and effort costs ($BIC_{hb}=$ $-1583$; $p<0.001$, Bayes factor; $pxp_{hb}=0.0001$). The additive model performed better for all of the 20 participants.

Model performance in fitting participant choices was also compared to performance when fitting choices made by a random decision maker. Comparison of the negative log-likelihood values confirmed that fits based on the participant choices were significantly better than fits to choices made by a random decision maker ($nLL_{participant}=$ 24.08 [19.07 29.09], $nLL_{random}=102.45$ [101.89 103.02], paired t-test, $p<0.001$). Individually, fits to each of the twenty participants outperformed fits to a random decision maker.

*Individuals tended to under-weight tested probabilities*

The second free parameter analyzed was $\gamma$ , which is a measure of how an individual weighted the probability of the risky decision. Eighteen of the twenty participants exhibited a $\gamma < 1$ (Figure 3.4B, green lines). The average $\gamma$ across participants was 0.61 [0.42 0.80], which was significantly less than 1 (independent t-test, $p < 0.001$, Figure 3.4B). Thus most participants over-weighted small probabilities and under-weighted large probabilities. This observation matches previous findings in similar tasks involving risky decisions (Tversky and Kahneman 1992; Abdellaoui 2000; Vrecko and Langer 2013).

*Full model matches decision-making tendencies across changing effort and probability*

Parameter fits to individual participants were validated by comparing the winning three-parameter model's predicted choices to each participant's choices. Similar to the behavioral data, as the effort cost of the lottery increased, the frequency of the model choosing the lottery decreased (Figure 3.3C, dashed lines, $\beta=0.85$, $p < 0.001$). Also, as the probability of having to perform the lottery increased, the frequency of the model choosing the lottery decreased (Figure 3.3D, dashed lines, $\beta=1.15$, $p < 0.001$). Model-predicted choices were indistinguishable from actual choice data (Linear mixed effects model, *Effort*: $p = 0.845$, *Probability*: $p = 0.667$).

*Decision-making tendencies were consistent across multiple days*

All individuals that returned for a second round of decision making (n=13) exhibited choice behavior that was consistent with the first visit. No differences were

observed between parameter fits across days (Figure 3.5, mean±95CI, $\varepsilon_{day1}$ = 0.95 [0.76 1.14], $\varepsilon_{day2}$ =1.11 [0.64 1.58], p = 0.49; $\gamma_{day1}$= 0.62 [0.41 0.83] , $\gamma_{day2}$ = 0.80 [0.45 1.15], p = 0.23). A linear regression was performed to determine the slope between $\varepsilon$ on day 1 and day 2. The slope was 1.13 [0.64 1.63], and could not be distinguished from unity ($\beta$=1). Similar findings were observed with $\gamma$ . The slope of the relation between $\gamma$ on day 1 and day 2 was not significantly different from unity (slope = 1.22 [0.78 1.66]). Therefore decision-making strategies executed on the initial day of testing were similarly enacted on subsequent days.
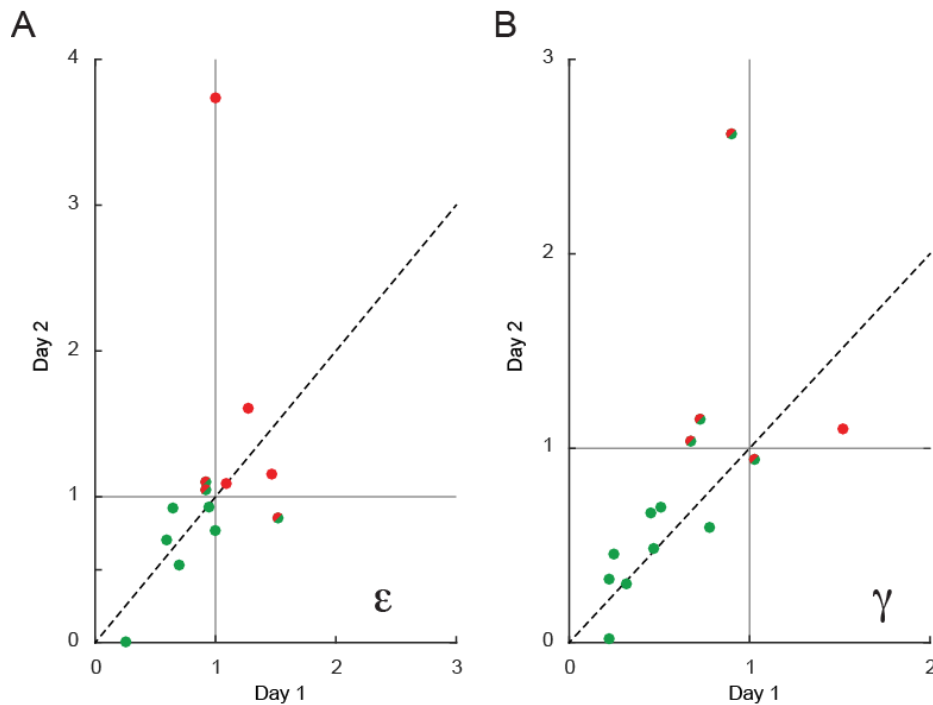


Figure 3.5 Parameter stability of thirteen participants measured between behavior sessions 1 and 2 describing A) the subjective value of effort and B) probability weighting. Horizontal values represent parameter values measured on first behavioral session and vertical values represent parameter value on second behavioral session. Values along the dashed unity line represent identical values between sessions. Green markers indicate individuals with parameter values below 1 in both days. Red markers indicate values greater than 1 for both days. Red/Green markers indicate parameters

greater than 1 on one day and less than one on the other. Slopes for both $\varepsilon$ and $\gamma$ were statistically indistinguishable from unity, suggesting decision-making strategies of the group were conserved across days.

*Cost of time and accuracy were unaffected by changing effort*

Increasing resistance introduces potential costs in addition to effort that may affect decision-making behavior. Two costs that may change with resistance are time and accuracy. The experimental protocol controlled strictly for time, which was confirmed by the lack of any difference in average reaching velocity across conditions ($V_{ave}$= 0.34m/s [0.33 0.36], $F(4,76)$=1.81, $p$=0.136).

To minimize the effect of accuracy requirements on decision making, I created a large target (15cm wide) so that across all resistances, the probability of missing the target was extremely low. In all conditions, participants tended to reach to the center of the target with a small absolute horizontal deviation of 5.93 [4.95 6.91] mm. There was an effect of condition on absolute deviation ($F(4,76)$=30.6, $p$<0.001). When uncorrected, post-hoc analysis revealed the null resistance (0 Ns/m) to have a larger absolute deviation (8.33 [7.30 9.36] mm) compared to the other four conditions (5.33 [4.37 6.29] mm) (p's=0.041, 0.045, 0.025, 0.016). These differences were lost when a Bonferroni correction was implemented. Since all of these deviations still led to on-target movements, no corrective feedback was provided to the participants that would compel them to alter their behavior.

## 3.5 Discussion

In this first chapter, I quantified subjective valuation of effort in a moderately effortful movement task. Using a novel approach, I considered effort to be represented by the metabolic cost required to perform the movement, and explicitly measured that metabolic cost via expired gas analysis. My protocol used a risky decision-making task that allowed us to map utility directly onto effort in the appropriate units of energy (Joules) without the confound of intermediate conversions such as money, force, number of movement repetitions, and time. As such, my approach provided new insights into how effort is truly represented in movement tasks, and avoided the inherent inaccuracies and approximations in other approaches that are less naturalistic and never truly measure effort. Therefore, these results provide a unique window into how physical effort is considered when choosing between effortful movements.

With increasing effort costs, are additional increments in objective effort overvalued or undervalued? I found that there was a significant nonlinearity in the relationship between effort and its subjective value. The shape of this nonlinearity varied idiosyncratically across subjects, with no consistent distortion observed. Approximately an equal number of participants overvalued and undervalued effort, with the group average indicating an objective valuation of effort. Despite the large variability across individuals, this function remained fairly robust within an individual across testing days.

Only recently have scientists begun to probe the effects of effort costs on decision making. Previous work delving into physical effort has tended to focus on how effort costs discount reward, producing an overall utility for each prospect (Phillips et al. 2007; Schmidt et al. 2008a; Prévost et al. 2010; Klein-Flügge et al. 2015; Morel et al.

2017). Candidate utility functions have been proposed that take either a hyperbolic or quadratic shape. The use of a hyperbolic function stems from the idea that effort discounts reward in the same manner that time discounts reward. However, there is no conclusive evidence supporting such a function. Moreover, we find that a model of utility in which reward is discounted hyperbolically by time, performs significantly worse in explaining subject choices. The quadratic shape is equivalent to setting the parameter $\varepsilon=2$ in our analysis. This shape was derived on the premise that the subjective value of effort costs increases supralinearly, drawing from findings in the perception literature (Stevens and Cain 1970; Borg 1982). My results demonstrate that in the case of moderately effortful tasks, effort sensitivity does not consistently increase supralinearly across participants.

There are a few possible explanations for the apparent discrepancy between my findings and those recent studies (Hartmann et al. 2013; Klein-Flügge et al. 2015). First, I probed a lower range of effort requirements. Both Hartmann et al. and Klein-Flugge et al. probed effort levels up to approximately maximum effort. My goal was to identify effort valuation in moderately effortful tasks similar to those experienced in common daily activities. It is possible that the nonlinearities previous studies observe in effort valuation may only begin to emerge only at near-maximal effort levels as a result of pain, discomfort, or force saturation effects.

Another difference between my study and previous ones on effort-based decision making is the influence of subjective valuation of reward. Many studies make the assumption that the subjective valuation of the reward increases linearly with an increase in reward magnitude. Levy et al. (2011) found that different rewards including

money, food, and water are all valued nonlinearly. To minimize the possible confound of subjective reward values, my paradigm was designed in a manner void of explicit rewards. Participants were instructed to make decisions based solely on effort expenditure. While monetary compensation was provided to all participants for completing the experiment, it was distributed equally and independently of choice behavior.

A recent study by Morel and colleagues (2017) examined the role of physical effort in reaching movements, without the confound of monetary rewards. Notably, they observed a near quadratic sensitivity to effort, when effort was quantified as the resistive force. A possible reason for the apparent contradiction with my results is that effortful movements were compared in the same currency by presenting participants with a choice between one movement against a given resistance versus two movements at a different resistance. The assumption was made that the effort of two movements was double the effort of one movement. However, it is not known whether this assumption holds for metabolic cost. Rather than identifying doubling points, here I used probabilities to modulate the value of the options while maintaining the same currency (Joules), and also measured metabolic cost.

Prior investigations have also used proxies for effort modulation rather than directly measure metabolic cost. Common proxies have included grip-force, number of buttons pressed, and sizes of obstacles scaled (Stevens and Cain 1970; Hartmann et al. 2013; Klein-Flügge et al. 2015). While metabolic cost is likely to increase in all these cases, the shape of the relationships have not been identified. As such, any nonlinearities observed may be a result of a nonlinear mapping between metabolic cost

and the proxy employed. A novel method introduced in my study is that I measured changes in effort based on the amount of metabolic energy used to perform each task, allowing me to directly quantify the relationship between the objective and subjective costs of effort.

Similar to other effort paradigms, I added a probability cost. Probability was necessary to make lottery combinations that were similar in subjective value to the reference option. To account for known distortions in probability weighting, I used a single parameter Prelec function (Prelec 1998). Little is understood about how this parameter behaves in losses, but when comparing our results to a similar function originally proposed by Tversky and Kahneman (1992), I found qualitatively similar and statistically indistinguishable results (Tversky and Kahneman 1992; Abdellaoui 2000; Vrecko and Langer 2013)[2,36,37]. This consistency strengthens my conclusion on effort valuation by considering the effects caused by distortions in probability weighting.

The theoretical framework of optimal feedback control has significantly advanced our understanding of movement control (Todorov 2004). A key component of such models is the incorporation of a cost function that includes an effort cost. The effort cost has historically been represented as the sum of the squared forces or motor commands required to generate the movement. The quadratic term is largely due to mathematical convenience, since experimental results in both humans and other animals performing isometric force tasks have shown that effort costs, measured as metabolic cost, increase with the integral of absolute force, not squared force, over time. One possible justification for the quadratic term is that while effort costs increase linearly with force, the subjective value of effort may increase supralinearly with force. However, my results

demonstrate that on average, effort costs are valued objectively, and suggest that these cost functions should consider this in order to more accurately represent objective effort costs.

Recent models of decision making and movement control predict that as the effort requirements of a movement of a given distance increase, the speed with which that movement is executed should decrease (Mazzoni et al. 2007; Qian et al. 2012; Rigoux and Guigon 2012; Shadmehr et al. 2016). Indeed, behavioral findings have confirmed this prediction in reaching tasks (Gordon et al. 1994). Work by Mazzoni et al. (2007) suggests the slower reaching speeds observed in Parkinson's patients is a result of an exaggerated cost/benefit ratio. Following up on these observations, it would be interesting to determine whether differences in sensitivity to effort costs in a healthy population could explain inter-individual variability in preferred movement speeds.

## 3.6 Conclusion

The findings presented in this chapter demonstrate that there are idiosyncratic distortions in an individual's sensitivity to effort costs in a low-effort task, with some individuals showing increasing sensitivity to effort and yet others exhibiting diminishing sensitivity. However, on average individuals valued effort objectively, in contrast to previous observations of a quadratic valuation. Together, these findings provide the first quantification of effort valuation in reference to an objective physiological effort cost, and reveal an objective valuation in low-effort reaching tasks representative of activities of daily life.

# CHAPTER 4

# CONTRIBUTIONS OF METABOLIC AND TEMPORAL COSTS TO HUMAN GAIT SELECTION

## 4.1 Abstract

Humans naturally select several parameters within a gait that correspond with minimizing metabolic cost. Much less is understood about the role of metabolic cost in selecting between gaits. Here, I asked participants to decide between walking or running out and back to different gait specific markers. The distance of the walking marker was adjusted after each decision to identify relative distances where individuals switched gait preferences. I found that neither minimizing solely metabolic energy nor minimizing solely movement time could predict how the group decided between gaits. Of the twenty participants, six behaved in a way that tended towards minimizing metabolic energy, while eight favored strategies that tended more towards minimizing movement time. The remaining six participants could not be explained by minimizing a single cost. I provide evidence that humans consider not just a single movement cost, but instead a weighted combination of these conflicting costs with their relative contributions varying across participants. Individuals who placed a higher relative value on time ran faster than individuals who placed a higher relative value on metabolic energy. Sensitivity to temporal costs also explained variability in an individual's preferred velocity as a function of increasing running distance. Interestingly, these differences in velocity both within and across participants were absent in walking, possibly due to a steeper metabolic cost of transport curve. I conclude that metabolic cost plays an essential, but not exclusive role in gait decisions.

## 4.2 Introduction

Humans generally walk at slower speeds and run at faster speeds. In walking, metabolic cost when represented as a rate, increases nonlinearly as a function of velocity. Transforming metabolic rate to metabolic cost per distance, i.e. cost of transport (COT (Schmidt-Nielsen 1972)) reveals a U-shaped curve with the minimum roughly corresponding to the preferred walking velocity of humans (Ralston 1958; Browning et al. 2006) and other animals (Hoyt and Taylor 1981; O'Neill 2012) (Figure 4.1A). In running, recent evidence suggests that the metabolic rate also increases nonlinearly (Steudel-Numbers and Wall-Scheffler 2009; Tam et al. 2012; Willcockson and Wall-Scheffler 2012; Batliner et al. 2018) and that this curved relationship, while much shallower than in walking, may influence how individuals select running velocity (Long and Srinivasan 2013; Rathkey and Wall-Scheffler 2017).

Metabolic cost has also been shown to play an important role in establishing how we select between gaits. When instructed to traverse fixed distances in a constrained time, humans allocated the relative time walking and running and the velocities at those gaits in a manner that minimized total metabolic energy expenditure (Long and Srinivasan 2013). When moving on a treadmill with increasing velocity, transitions between walking and running gaits tend to occur at velocities close to where the respective COT curves intersect (Margaria, R 1938, 1976; Hoyt and Taylor 1981), which for human walking and running is found at approximately 2.25 m/s (Figure 4.1A) (Margaria, R 1938, 1976).

The metabolic cost of locomotion has also been shown to play an essential part in explaining how animals forage for food in their environment (Pyke et al. 1977;

Bautista et al. 2001; Wilson et al. 2001; Shepard et al. 2013). Recent models inspired by optimal foraging theory quantify the utility of each movement according to the interactions between minimizing the costs of the movement (both time and energy spent) and maximizing the benefits of the movement outcome (primary and secondary reinforcers) (Rigoux and Guigon 2012; Shadmehr et al. 2016). An essential component of these models is that movements take time, which negatively influences utility (Choi et al. 2014). This effect of time on movement utility is subjective, with certain individuals exhibiting a much greater sensitivity to temporal costs than others (Choi et al. 2014).

We lack a clear understanding of how gait preferences are established when movement time is unconstrained. In the present study, I attempted to understand how metabolic energy and time interact when choosing between walking and running gaits. I hypothesized that there would be situations where running was preferred over walking, despite the greater COT for running. Furthermore, I expected that preferences would best be explained using a utility model that does not exclusively minimize either metabolic cost or time, but instead would be based on a participant-specific combination of these two costs.

## 4.3 Methods

*Theoretical development*

I postulate that when an individual considers whether to walk or run, they behave in a way that maximizes movement utility (*J)*, meaning they balance minimizing costs associated with each gait while maximizing reward as a result of successfully completing the trial. When deciding between performing different movements, the

observed preference is assumed to be the option that carries greater utility. In the current paradigm, I assumed that changing the cumulative distance covered for a movement affected the utility of the movement. I introduce several candidate models to predict relative distances where the utility of each gait is equal to the other ($J_{walk}=J_{run}$) and then compare each model's predictions to observed gait preference of each individual. I refer to the walking and running distances where participants switch preferences between gaits as indifference points.

To emphasize the differences across candidate models, I represent indifference point predictions according to a linear function where the walking component of the indifference point ($D_w$) is predicted as a function of the running component ($D_r$) with the unity line of this space representing walk/run combinations of equal distance (Figure 4.1B, dashed line). I refer to the slope of this linear function as the indifference slope. Distance pairs falling above the indifference slope of each model predict a greater utility for running and combinations below the indifference slope predict greater utility for walking. At no time during this experiment did I introduce or manipulate any form of explicit reward as a result of completing a walk or run trial. Considering this, the proposed models assume that participants made decisions with the goal of exclusively minimizing costs. I present four possible models of utility, each making unique predictions for the slope of the walk/run indifference function. These candidate models are based on (1) minimizing COT, (2) minimizing cumulative total amount of metabolic energy, (3) minimizing cumulative total of movement time or (4) minimizing total time per distance (maximizing velocity). These four models each require some combination

of the total distance traveled for each gait, average velocity for each gait ($V_w$ for walk, $V_r$ for run), and/or average metabolic rate for each gait ($\dot{E}_w$ for walk, $\dot{E}_r$ for run).
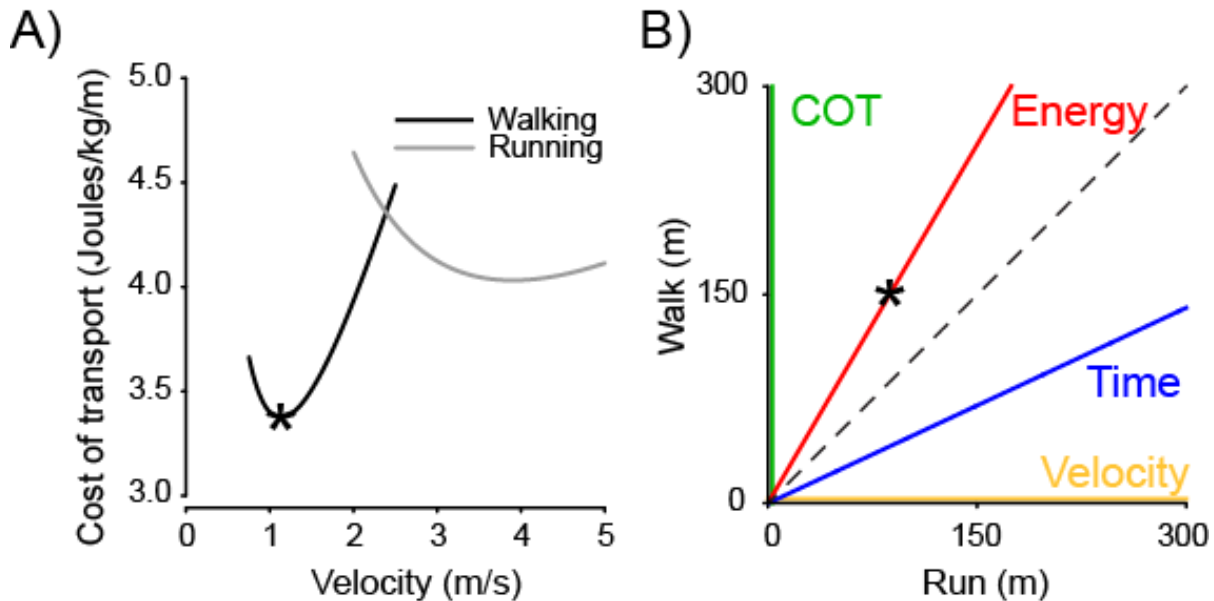


Figure 4.1 Model predictions. A) Metabolic cost of transport (COT) normalized by body weight for walking (black curve) and running (gray curve) using values reported in (Long and Srinivasan 2013). The asterisk indicates that an individual minimizing COT would always choose to walk. B) Model predictions for the slope of the indifference points. Minimizing COT predicts an individual would prefer to walk rather than run when allowed to choose their own velocities regardless of relative walking and running distances (green vertical line parallel vertical axis). The indifference boundary for minimizing total metabolic energy (red line) lies above unity suggesting that walking a greater distance carries an equal cost in terms of total metabolic energy as running a shorter distance. The indifference line for time (blue line) lies below unity suggesting that walking a shorter distance carries an equal cost in terms of time compared to running a longer distance. Walk/run combinations above model boundaries would predict a preference to run whereas combinations below the line would predict a preference to walk. A model based on minimizing time per distance (maximizing velocity) would always predict that an individual would run regardless of relative distances (gold horizontal line). All predictions assume walking and running at constant, self-selected velocities where the walking velocity is slower than the running velocity. The asterisk represents a theoretical indifference point for an individual who minimizes total metabolic energy. For this individual, running 100 meters and walking 150 meters have equal utility.

*Minimizing Cost of Transport ($J_{COT}$)*

Calculating the indifference slope based on minimizing COT is dependent on minimizing the total metabolic energy normalized per unit distance. One way to calculate COT is to divide the metabolic rate by velocity:

$$J_{COT_x} = -\frac{\dot{E}_x}{V_x}$$

[ 4.1 ]

Here, x denotes a placeholder for either walking (w) or running (r). A model of COT is exclusively determined by the velocity of the gait, which when at a constant velocity, is independent of changes in either total distance or total time. Self-selected walking velocities generally elicit lower COT than self-selected running velocities. Thus, this model would predict that an individual would always prefer to walk, regardless of the relative walking and running distances (Figure 4.1B, green line parallel vertical axis). The negative sign in this model and subsequent models indicates that maximum movement utility is achieved by minimizing these costs.

*Minimizing total energy ($J_{energy}$)*

Predicting indifference boundaries by minimizing total energy is based on both the COT [eq. 4.1] and total distance covered using each gait. Measuring utility as a minimization of total energy can be achieved by calculating the COT of moving and multiplying that cost by the total distance moved:

$$J_{energy_x} = -COT_x D_x$$

[ 4.2 ]

Predicting indifference according to minimizing total energy yields a linear function where walking distance is predicted by:

$$D_w = \frac{COT_r \, D_r}{COT_w} \qquad\qquad [\,4.3\,]$$

When predicting walking distance as a function of running distance, a utility model that minimizes total energy will predict a slope above the line of unity indicating that walking a longer distance at a lower COT will be equal to running a shorter distance at a higher COT (Figure 4.1B, red line).

*Minimizing total time ($J_{time}$)*

A utility model that is based on minimizing movement time requires two measurements to predict an indifference point, the velocity and distance of each walking and running bout:

$$J_{time_x} = -\frac{D_x}{V_x} \qquad\qquad [\,4.4\,]$$

Representing the minimization of movement time as a potential utility model to predict walking distance results in the function:

$$D_w = \frac{D_r \, V_w}{V_r} \qquad\qquad [\,4.5\,]$$

When predicting walking distance as a function of running distance, a utility model that minimizes total time will predict a slope for indifference below the line of unity indicating that walking a shorter distance at a slower velocity has equal utility as running a longer distance at a faster velocity (Figure 4.1B, blue line).

Maximizing velocity ($J_{vel}$)

Lastly, we consider a possibility where maximizing utility would always predict a preference to run. A utility based on this prediction can be described by minimizing total time per unit distance (maximizing velocity) and can be represented simply as:

$$J_{vel_x} = V_x \qquad\qquad [4.6]$$

This utility would result in a horizontal line (Figure 4.1B, gold line) and therefore would predict no change in equivalent walking distance as a function of increasing running distance.

*Participants*

Twenty participants (12M, 8F, 19-32 years, 73±12 kg) gave written informed consent approved by the University of Colorado Institutional Review Board before participating in the experiment. All participants reported light-intensity exercise (Riebe et al. 2015) at least once a week and no neurological, cardiovascular, or biomechanical maladies. Experimentation took place in a lighted, climate-controlled, indoor track facility.

*Task*

Upon arrival, all participants first completed two laps around a 200-meter track. The first lap was performed at a self-selected walking velocity and the second lap at a self-selected running velocity. When selecting their running velocity, participants were instructed to select a velocity that they felt they could comfortably maintain for over one mile (~1.6km). During each lap, participants were instructed to explore different

velocities to find what they felt was most comfortable for each gait. Participants were instructed to use these walking and running velocities throughout the duration of the experiment.

The remainder of the experiment was designed to identify pairs of running and walking distances where running a given distance, $D_r$, was equally preferred to walking a given distance, $D_w$. These walk/run pairs of distances defined indifference points (Figure 4.1B, asterisk). To measure a single indifference point, participants completed 4 sets of trial triplets. A triplet consisted of a single walking trial, a single running trial, and a single choice trial (Figure 4.2A). In walking trials, participants walked out to an indicated walk distance and back. In running trials, they ran out to an indicated run distance and back. In choice trials, they were given the freedom to repeat either the previous walk or run trial. The first trial in a triplet was randomly assigned as either the run or walk trial and the last trial in a triplet was always a choice trial. Each block consisted of 4 triplets of trials and each participant completed 5 blocks, with every block representing a single indifference point. Importantly, before the start of the first block, all participants were explicitly informed that the remainder of the experiment would last a total of two hours and that their choice behaviors would not influence overall testing duration (i.e. choosing the shorter duration trial every time would not shorten the total time spent testing).

Figure 4.2B depicts the progression of one block of trials used to identify a single indifference point. The first triplet of trials in each block consisted of equal walk and run distances. Throughout a block, the run distance (Figure 4.2, red markers) was fixed. Walk distances (Figure 4.2, blue markers) were adjusted after each triplet of trials. The

direction of the adjustment was contingent on the participant's choice trial (Figure 4.2, gray regions). If the last choice was to run, the walk distance was *shortened* for the next triplet. If the last choice was walk, the walk distance was *lengthened*. The magnitude of the adjustment was greatest in response to the first choice and decreased with each subsequent choice. The adjustment after the first triplet was equal to the initial walk distance minus 20m (minus 10m in 40-meter run block). The adjustment after the second triplet was one half the initial walk distance and the adjustment after the third triplet was one quarter of the initial walk distance. No adjustment was made after the fourth (last) triplet.

I calculated a single indifference point upon completion of the fourth triplet in each block. The walk component of an indifference point was calculated at the end of each block by averaging the walk distances of the last walk choice and last run choice. The run component was equal to the tested running distance for that block. Five indifference points were calculated for each participant based on titrated walking distances equal to running distances of 40, 60, 80, 100, and 120m. The order of run distances was randomized for each participant.
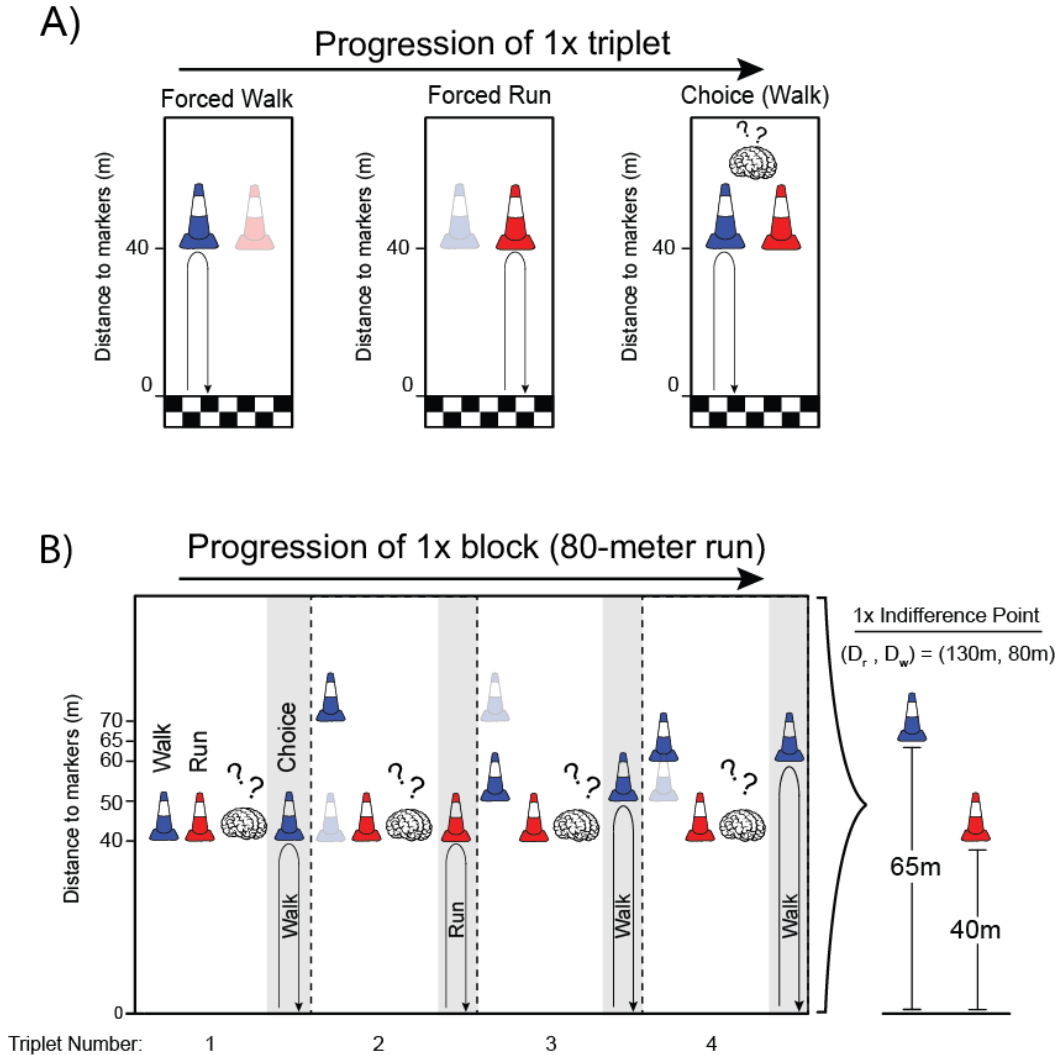
Figure 4.2 Protocol. A) Progression of a single triplet of trials. This example triplet began with a walk trial, where the participant walked to the blue marker and back. The second trial was a run trial where the participant ran to the red marker and back. The third trial was a choice trial where the participant thought about which previous trial they preferred and then repeated that trial. The first trial within each triplet randomly began as either a walk or run trial. The last trial of each triplet was always a choice trial. The decision to either walk or run influenced the distance of the walk cone on the subsequent triplet. B) Example progression of the 80-meter block. Each block consisted of completing four triplets of walk/run/choice trials. After each triplet, the walk distance was adjusted based on the previous decision. Dashed lines indicate start of a new triplet. To calculate the walk component of a single indifference point ($D_w$), we averaged the walk distances between the last run choice and last walk choice. The run component of the indifference point ($D_r$) was based on the run distance, which was fixed within a block. Each new block used a different fixed run distance. Note that the distances on the vertical axis represent the distance to the marker. The actual distance covered was two times the distance to the marker resulting from the participant moving out and then returning back to the start in a single trial.

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*Model Predictions*

  I measured the average walking and average running velocity at each block and used those values, along with the five tested running distances, to calculate walking distances that would result in an equal utility to running. A set of five walking distances were calculated for each proposed utility model. I then fit a line through each of these sets of walking distances using a simple linear regression. This resulted in a slope for each utility model that could then be compared to the observed indifference slope of each participant. Note that the slope predicting walking distance based on minimizing COT would result in a vertical line and a slope based on maximizing velocity would result in a horizontal line.

  To calculate the utility of each option, I did not directly measure metabolic COT, but instead estimated it according to eq. 4.1. Metabolic rate ($\dot{E}_x$) normalized by mass was estimated as a function of velocity from previously published equations (Long and Srinivasan 2013). Metabolic rate in walking was estimated according to the function:

$$\dot{E}_w = a_o + a_2 V_w^2 , \qquad\qquad [\ 4.7\ ]$$

where $a_o$=1.91 W/kg and $a_2$ = 1.49 W (m/s)$^{-2}$. Metabolic rate for running was estimated according to the function:

$$\dot{E}_r = b_o + b_1 V_r + b_2 V_r^2 , \qquad\qquad [\ 4.8\ ]$$

where $b_o$ = 5.17 W/kg, $b_1$ = 1.38 W (m/s)$^{-1}$ and $b_2$= 0.34 W (m/s)$^{-2}$ .


*Statistical Analysis*

  I used a simple linear regression based on each participant's indifference points to predict the indifference slope that explains walking distance as a function of running

distance when fit through the origin. I performed a Hartigans' dip test to measure whether the distribution of fitted indifference slopes was multimodal.

The best performing model for each individual was decided by comparing the 95% confidence interval of the slope fit through a participant's indifference points against the slopes estimated for each of the four models. To test whether the fitted indifference slope indicated an individual's desire to minimize time, I measured the correlation between an individual's fitted indifference slope and preferred gait velocity using a simple linear regression. I also explored whether individuals adjusted their preferred gait velocity as a function of distance and whether this adjustment was based on how an individual represented each cost. Due to the different walking distances experienced by each participant, this was achieved using a linear mixed effects model rather than a simple linear model with walking and running velocities predicted as a function of indifference slope and distance for each walking and running trial. All comparisons were conducted at a statistical level of α=0.05. Descriptive statistics are reported as mean ± SE.

## 4.4 Results

Participants made decisions between walking and running different combinations of distances. I adjusted the relative distances of walking and running after each decision until individuals were indifferent between performing either gait. I refer to these final combinations of distances as indifference points and assume that at those combinations the utility of walking is equal to the utility of running. I compared the fitted slope describing each participant's indifference points to slopes calculated from utility models

that minimize COT, minimize total metabolic energy, minimize total movement time, and maximize total velocity. Overall, my results suggest that the mechanisms responsible for how the group of individuals selected gait cannot be explained through the minimization of a single metabolic or temporal cost. Rather, participants minimize a weighted combination of these two conflicting costs, with the relative representation of each cost varying across participants.

*Cost only models fail to predict decision-making strategies across group*

Figure 4.3 illustrates how a single individual's gait decisions were used to calculate indifference points as a function of increasing running distance. The goal was to identify which utility model best represents the indifference slope where combinations of distances above the line predict a running gait (Figure 4.3, 'R' symbols) and combinations below the line would predict a walking gait (Figure 4.3, 'W' symbols).

I described an individual's preference for each gait by fitting a line through the estimated indifference points (Figure 4.3, black line). Fitted lines with relatively steeper slopes are more representative of minimizing total metabolic cost (Figure 4.3, red line) and relatively shallower slopes are representative of minimizing total movement time (Figure 4.3, blue line). Minimization of total COT cannot be described according to any slope because it predicts a preference to walk independent of any non-zero run distance (Figure 4.3, green line parallel vertical axis). Maximization of velocity also cannot be described according to any slope because it always predicts a preference to run (Figure 4.3, gold line parallel horizontal axis).
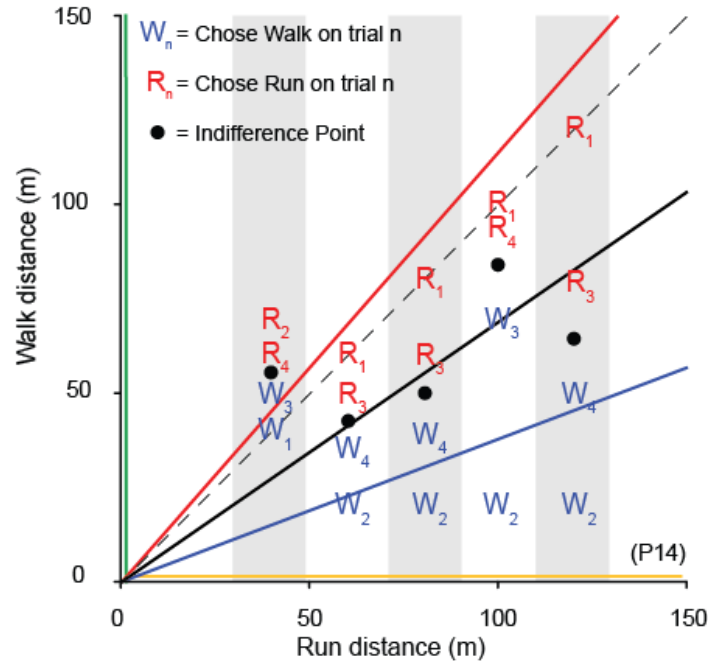
Figure 4.3 Depiction of how each block of triplets contribute to describing gait preference as a function of running and walking distance (representative participant, P14). The horizontal axis represents the run distance (m) of each decision and the vertical axis represents the accompanying walk distance (m). The preferred gait at each pair of distances is represented either as a 'W' if the participant preferred to walk or an 'R' if the participant preferred to run. The subscript accompanying each letter indicates at which triplet the choice occurred. The first decision of each block was always of equal walking and running distances (decisions along dashed unity line). The walk component of each indifference point (black markers) was calculated by averaging the walk distances of the last chosen run and last chosen walk trials. The run component was equal to the unchanged run distance within that block. Shaded bars are intended to help contain the groups of decisions made within each block. The black line represents the slope of the regression line fit through all indifference points. Model predictions for this slope are made by minimizing COT (green), total metabolic energy (red), total movement time (blue), and maximizing velocity (gold).

Across all participants, the average preferred walking velocity was 1.53±0.03 m/s and the average running velocity was 3.32±0.12 m/s. Using these velocities, I could predict walking distances as a function of running distance according to each proposed utility model. The average slope for the utility model minimizing total metabolic energy was equal to 1.16±0.01 meters of walking for each meter of running. When minimizing

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total time, I estimated a much smaller average slope of 0.46±0.01 meters of walking per each meter of running.

Every participant made at least one choice to run in each block, a choice that is counter to the minimization of COT. The walking component of each indifference point increased as a linear function of the running component in all participants except for P8 ($r^2$=0.72±0.05, range=0.29-0.99). Indeed, not a single participant's fit exhibited confidence intervals that encompassed the COT indifference slope (Figure 4.4, green vertical line). Six of the 20 participants had 95% CIs that encompassed minimization of total energy (Figure 4.4, red line; P1, 2, 4, 5, 18, 20). Eight participants had 95%CIs that encompassed minimization of total time (Figure 4.4, blue line; P9, 10, 11, 12, 13, 15, 16, 17). One participant had a slope that was best predicted by maximizing total velocity (Figure 4.4, gold line; P8). The remaining five participants had indifference slopes that could not be explained by any of the proposed utility model (P3, 6, 7, 14, 19). No single participant had 95%CIs that encompassed more than one model. I can also apply a less-stringent criteria and assign a model to each participant based instead on proximity of the indifference slope to the nearest utility model, calculated as the absolute difference between the participant's indifference slope and each utility model's slope. In this case I found that eight participants were best explained by total energy, eleven were best explained by total movement time, and one was best explained by maximizing velocity.

While it appears that no single cost was able to explain decision making across our entire group of participants, it is possible that clusters of participants may have selected a single cost (energy or time). If this was the case, I would expect there to be a

clear bimodal distribution in slopes between the participants that minimized energy and the participants that minimized time. I found that the slopes across our participants (not including P8) ranged from 0.3 to 1.8. When testing across this range of slopes, I found the distribution to be unimodal (Hartigans' dip test, p=0.44). Based on this result, I cannot conclude that there were two discrete time and energy strategies. Instead, there was a range of relative weightings between these costs.
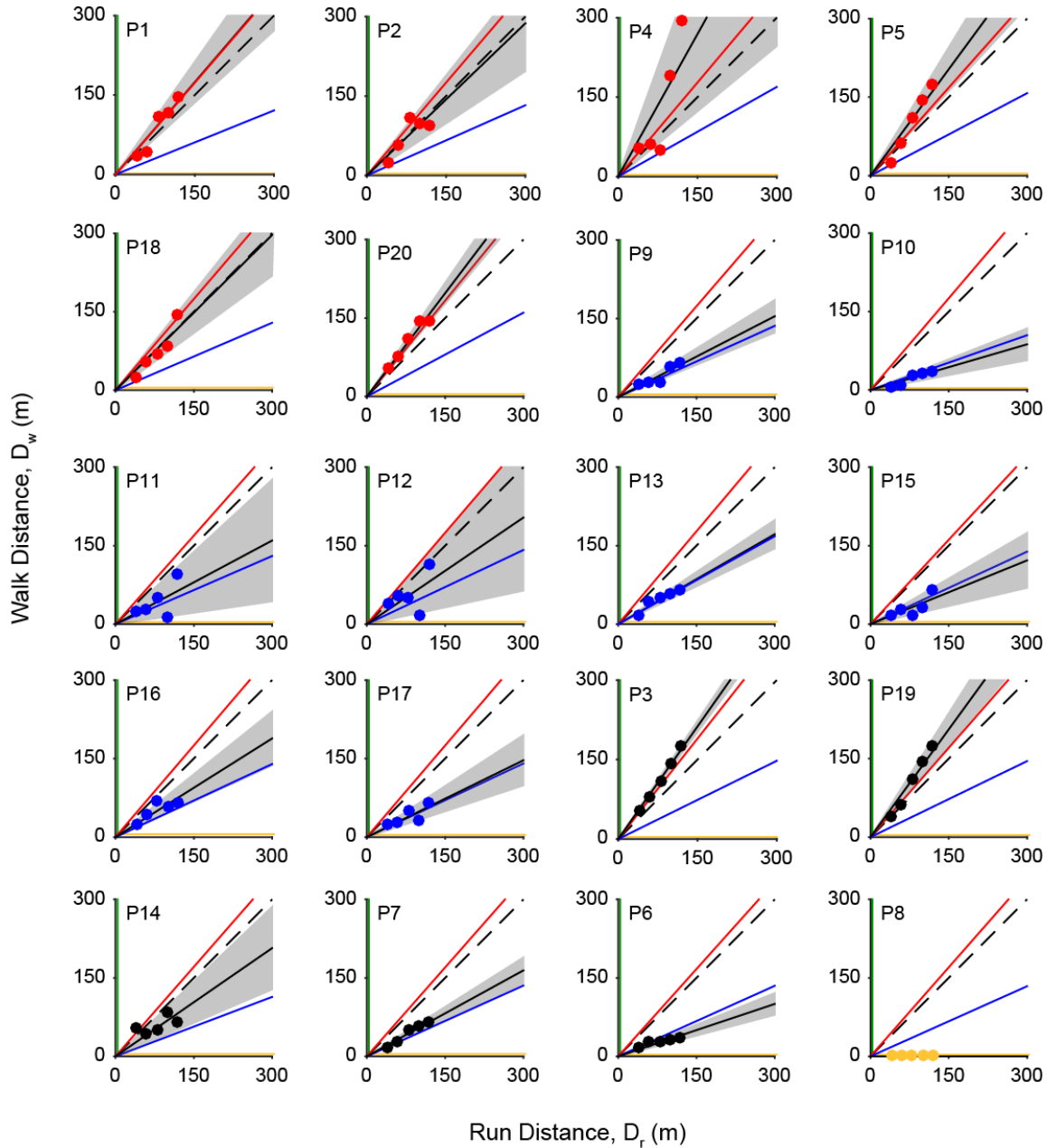
Figure 4.4 Model predictions for walk and run combinations of equal utility. Green lines represent indifference slope predictions based on minimizing COT, red lines represent predictions for minimizing total metabolic energy, blue lines represent predictions for minimizing total time, and gold lines represent predictions for maximizing velocity. Black line and shaded gray areas represent best fit and 95% confidence intervals for the indifference slope according to the estimated indifference points. Six participants had CIs that fell within the total energy model (indicated by red indifference points), eight participants had CIs that fell within the time model (blue indifference points), and five participants had CIs that did not fall within any of the cost minimization models (black indifference points). Participant eight (P8) always chose to run, independent of any manipulations to walk distances (maximized velocity, indicated by gold indifference points). Axes are equally scaled across all participants.

*Including time for waiting does not improve performance of total energy model*

The duration of the entire experiment was constrained to 2 hours and was unaffected by an individual's preferences between gaits. One consequence of preferring the gait with the shorter duration was that there was a subsequently longer waiting time before the next trial. To consider the metabolic consequences of waiting, I calculated the difference in movement time between the shorter and longer movement, multiplied that difference by a typical metabolic rate for standing at rest ($\dot{E}_{wait}$=1.22 W kg$^{-1}$ (Long and Srinivasan 2013)), and added that cost to the total energy of the movement with the shorter duration. Considering the added metabolic cost of waiting, the average total energy slope increased to 1.24±0.13 meters of walking per meter of running. This new total energy model still only falls within the 95% CI of the indifference slope for four participants (P1, 5, 19, 20), indicating that minimizing total energy alone does not appear to represent the utility model used for gait decisions in this group of participants.

*Individuals who minimized time did not walk faster, but they did run faster*

Minimization of total energy predicts a relatively steep indifference slope, indicating that moving slower (walking) for longer distances is equal to moving faster (running) for shorter distances. Minimizing total movement time makes an opposite prediction, indicating that moving slower for shorter distances is equal to moving faster for longer distances. An individual who considers time in their decisions will have a shallower slope to describe their indifference points. Assuming gait velocity reflects the desire to minimize movement time, we tested whether there was a correlation between each participant's indifference slope and their self-selected gait velocity. I found no

correlation between an individual's indifference slope and their average preferred walking velocity (Figure 4.5A, $r^2$=0.038, p=0.452), but I did find a moderate negative correlation between an individual's indifference slope and their average preferred running velocity (Figure 4.5B, $r^2$=0.325, p=0.009).
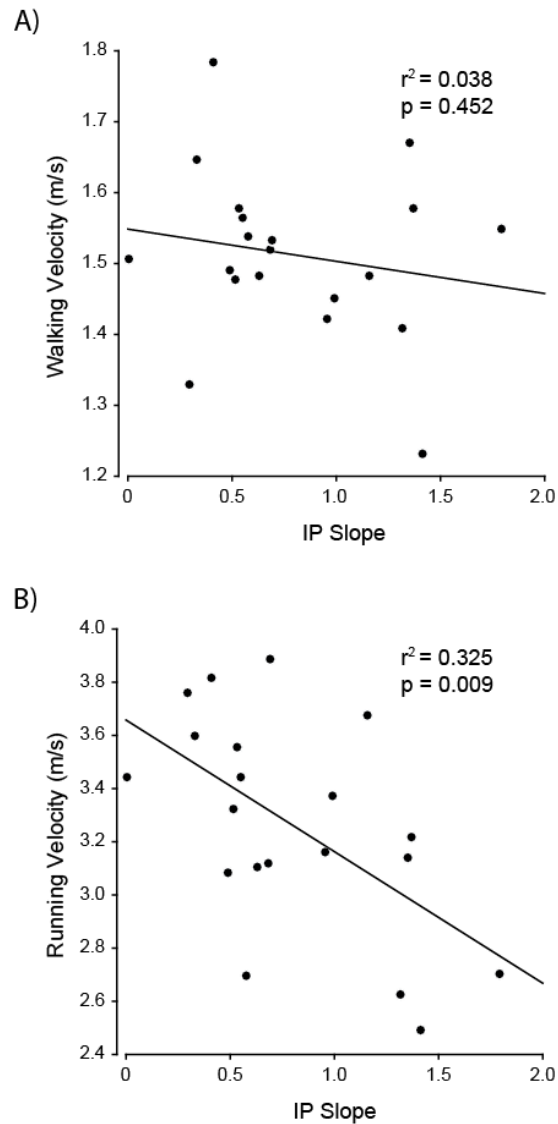


Figure 4.5 Correlations between indifference point (IP) slope and average preferred gait velocity (m/s) in A) walking and B) running. Each marker indicates a single participant.

*The distance of a running trial influenced preferred running velocity*

The range of walking distances was established according to individual gait preferences during choice trials. Across all participants, distances for a single walking trial ranged from 5 to 310 meters. The length of each running trial was the same for all participants and ranged from 40 to 120 meters. I would predict that individuals only sensitive to minimizing total metabolic energy (steeper slopes) would adapt a preferred gait velocity independent of total distance. For individuals willing to discount metabolic energy to decrease total movement time, I would expect preferred velocities to increase (become more metabolically costly) at greater distances to offset the added temporal costs of longer movements.

I performed a linear mixed effects regression to explain average gait velocities using distance and indifference slope as predictors. To minimize the influence of acceleration on average velocity, I excluded trials that were shorter than 30 meters (15 meters out and 15 meters back). This resulted in the removal of 88/380 trials across all participants, all of which were walking trials. With the remaining trials, I observed that walking speed was unaffected by either walking distance, indifference slope, or an interaction of the two predictors ($\beta_o$=1.601ms$^{-1}$, p<0.001; $\beta_{distance}$=0.001s$^{-1}$, p=0.052, $\beta_{IP}$=-0.114, p=0.123, $\beta_{interaction}$=-0.007, p=0.160). Contrary to the absent effects of distance on preferred walking velocity, I found a positive relationship between preferred running velocity and running distance ($\beta_o$=3.037ms$^{-1}$, p<0.001; $\beta_{distance}$=0.008s$^{-1}$, p<0.001, $\beta_{IP}$=-0.264, p=0.158) meaning that preferred velocity increased when running over longer distances (Figure 4.6), however the extent of this increase depended on the indifference slope of the individual ($\beta_{interaction}$=-0.004, p<0.001). Specifically, individuals

who placed a higher value on time (shallow slopes) chose a faster running velocity in response to longer distance tasks compared to individuals who placed a lesser value on time (steep slopes).
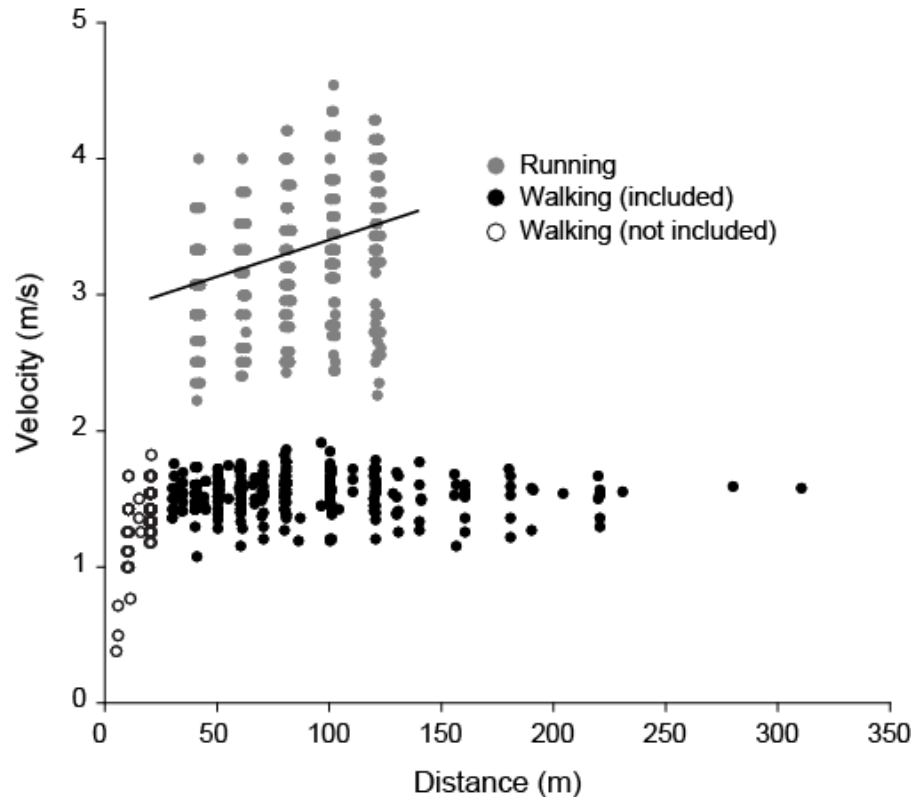


Figure 4.6 Relationship between preferred gait velocities (m/s) and total distance (m). Walking velocity was modeled as a function of distance using data points that were measured at or above a distance of 30 meters (filled circles). Any walking trials below 30 meters were not included in the fit (open circles). Across fitted trials, walking velocity was on average 1.57±0.03m/s and did not change as a result of increasing distance. Running velocity was also modeled as a function of distance and included all 380 running trials (gray filled circles). The black line is the model prediction for the median fitted indifference slope indicating that running velocity generally increased when trials required moving further distances. Graphically, all running and walking points were given a small amount of artificial noise along the horizontal axis to indicate regions where multiple trials were completed at identical velocities.

*Preferred gait velocity and decision-making tendencies were unaffected by the 2-hour duration of the experiment*

Within the two-hour duration of the current experiment, participants completed 60 combined trials of walking and running. This amount of locomotion introduces the possibility that individuals may have become fatigued, changing how movement costs were relatively weighted throughout the course of the experiment. To detect potential effects of fatigue, I measured changes in velocity for each gait as a function of block and observed that changes in both walking and running velocities were on average consistent throughout the entire experiment (Figure 4.7, rmANOVA, main effect of block, walking, $F_{(4,72)}=0.789$, $p=0.536$; running, $F_{(4,72)}=0.01$, $p=0.99$). This result suggests that if preferred velocity reflects how an individual weighs movement costs, the weighting of these costs was consistent throughout the experiment.

I also tested whether the frequency of choosing either gait changed across blocks. Independent of relative walk and run distances, the probability that a participant chose to walk was $45.53\pm0.51\%$ and this frequency was consistent throughout the duration of the experiment, (rmANOVA, main effect of block, $F_{(1,360)}=0.420$, $p=0.518$). These results further provide evidence that the duration of the experiment did not affect how an individual considered metabolic energy and movement time when selecting between gaits.
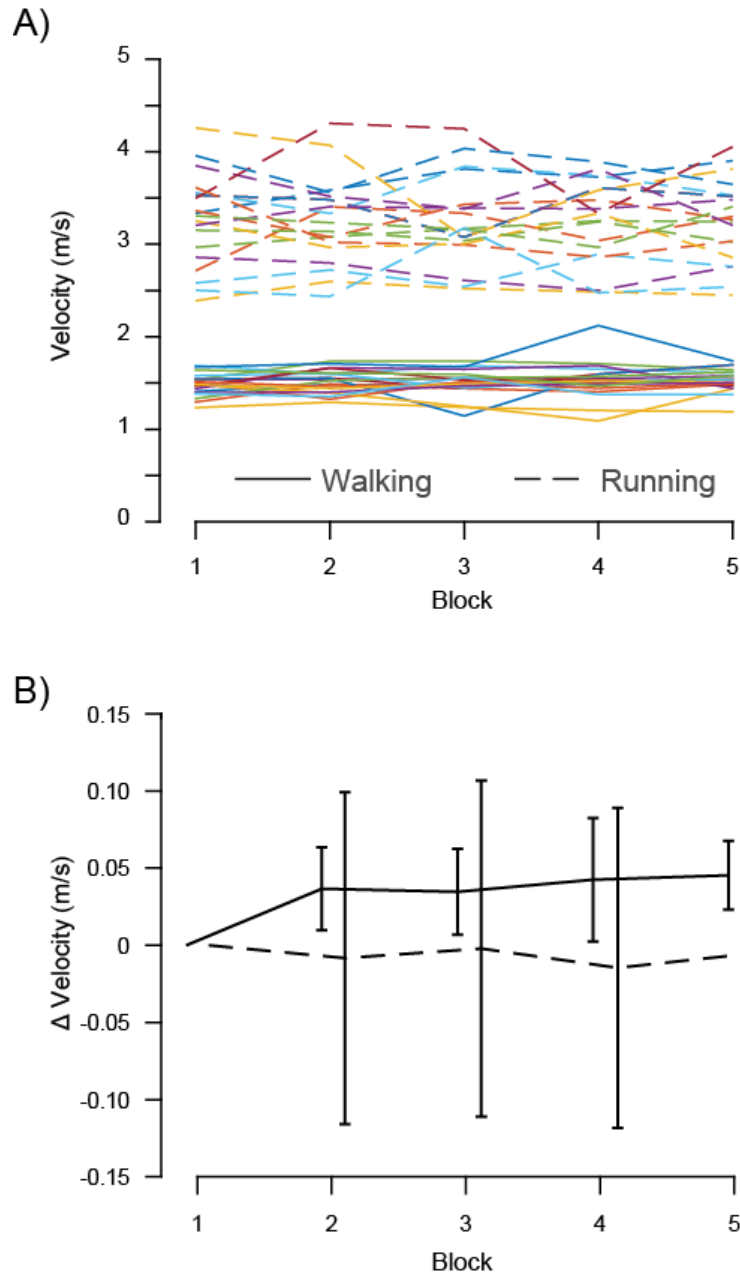
Figure 4.7 Effect of block on preferred walking velocity (solid line) and running velocity (dashed lines). A) Colored lines represent walking and running velocities for individual participants. Across the group, there was a much larger spread of preferred running velocities when compared to the spread of walking velocities. B) Average change in walking and running velocities across blocks represented as difference from the average velocity of the first block.

## 4.5 Discussion

The primary goal of the present study was to explore how humans weighed changing metabolic and temporal costs when deciding between walking and running gaits. The protocol consisted of individuals making gait decisions across numerous combinations of walking and running distances. Their gait preferences allowed me to estimate indifference points, defined as walk and run distance combinations where the preference of performing a walking gait was equal to the preference of performing a running gait. I quantified the metabolic and temporal consequences of each gait at each distance to explore whether minimizing either cost explained gait preference. For each individual, walking distance was accurately described as a linear function of running distance, however the slope of this function varied widely between participants. When modeling each individual's set of indifference points, roughly a third of our participants had indifference slopes that corresponded with minimizing total energy, another third appeared to minimize total movement time, and the remaining third could not be explained by minimization of either cost. The diversity of gait preferences across the group meant that decision-making strategies were likely not a result of minimizing a single movement cost, but rather a participant-specific weighting of the two.

I used the slope of the regression line fit through each participant's observed indifference points to explain how each cost contributes to the total movement utility of each gait. A relatively steep slope predicted a strong weighting on metabolic energy with little cost for time. A relatively shallow slope predicted the opposite, a strong weighting on time with less cost for metabolic energy. I found an average slope across

participants of 0.83, falling below the slope predicted by the minimization of metabolic energy (1.16) and above the slope predicted by the minimization of time (0.46).

Several participants (n=8) had indifference slopes that indicated their decisions were influenced by movement time, despite being informed that their decisions would not impact the total duration of the experiment. One explanation for this behavior is that completing each trial had an arbitrary utility that decreased over time, a phenomenon classically referred to as temporal discounting (Mazur 1987; Myerson and Green 1995). Recent results have demonstrated a role for temporal discounting in selection of reach velocity (Shadmehr et al. 2016; Summerside et al. 2018), building upon a growing body of research in movement decision-making (O'Brien and Ahmed 2015, 2016). The magnitude of temporal discounting has been reported to vary substantially between humans, with this variability accurately predicting how quickly an individual will generate movements toward a reward (Choi et al. 2014). If temporal discounting influenced how my participants decided between gaits, I would expect their sensitivity to temporal costs to manifest in how they selected velocity for each gait. I found that the running velocity of each participant was moderately explained by their indifference slope. Specifically, individuals who had a greater tendency to minimize time (shallower slopes) also selected faster running velocities. I did not find any correlations between indifference slope and walking velocity.

For movements of a set distance, individuals may have chosen to move faster to minimize the loss in utility due to temporal discounting. However, increasing velocity also influences the total metabolic energy required for the movement and implies that increasing velocity above what is metabolically optimal only improves total utility if the

benefits of arriving earlier are greater than the penalty of moving at a higher metabolic cost of transport. The COT curve as a function of velocity is relatively steep in walking when compared to running (Figure 4.1A). These differences predict that decreasing movement time in walking would come with a greater increase in metabolic energy compared to a similar change in movement time when running. This may explain why I found that indifference slope predicted running velocity, but not walking velocity.

Temporal discounting can also explain variability in running velocities observed within each participant. Participants adjusted their preferred running velocity, but not their preferred walking velocity as a result of increasing distance. If I assume that individuals were exclusively minimizing metabolic energy, they would move at a velocity corresponding to the minimum COT independent of total distance. However, as previously highlighted, temporal discounting will lead to greater losses in utility for longer duration movements. Decreasing total movement time over a shorter distance requires a greater change in gait velocity when compared to the same decrease in time over a longer distance. However, this explanation fails to account for the shape of the temporal discounting function, which commonly predicts that a discrete change in duration has greater effects when applied at earlier time-points when compared to those same changes at later time points (Mazur 1987).

Another explanation for why individuals discount the metabolic cost of running may be because the activity of running itself may carry an implicit reward through improving mood or affect (Farrell et al. 1987; Ogles and Masters 2003). When a group of regular runners were prevented from exercising for a two-week period, they reported symptoms similar to what is observed in individuals who are suffering from the

withdrawal of addictive drugs (Morris et al. 1990). The neurological basis of this exercise influenced reward may be explained through the release of endocannabinoids, (eCB), neurotransmitters that are known to influence the release of dopamine in the reward pathways of the brain (Garland et al. 2011; Gillman et al. 2015). Within an individual, the level of eCB released increases with exercise intensity, however, when comparing across individuals, these responses appear independent of fitness level (Brellenthin et al. 2017).

My protocol involved all participants running between 40 and 120 meters per trial. In walking, depending on the decisions of each participant, distances ranged between 5 and 310 meters per trial. Orendurff et al. (Orendurff et al. 2008) reported that in healthy adults, over 90% of recorded movement bouts throughout the day involved taking fewer than 100 consecutive steps. Del Din et al. (Del Din et al. 2016) similarly reported that only 3% of movement bouts in healthy older adults had a duration of greater than 60 seconds. While my tested distances are within the range of what would be considered a representative movement bout, the actual limits of what a healthy adult human can cover are obviously much greater. Obtaining indifference points over a larger range of walking and running distances would allow for a better understand as to whether my assumption that utility increases linearly as a function of distance, or rather if distance interacts with the weighting between metabolic and temporal costs.

In each trial, participants had to ambulate to the indicated marker turn around and return. This exchange required 4 different moments of significant acceleration; an initial acceleration to preferred velocity, deceleration when approaching the marker, re-acceleration when leaving the marker, and a final deceleration at the end of the trial. In

longer movements, these accelerations likely had minimal impact on average velocity. However, when the movements were short, calculating average velocity as total distance over total time may not accurately represent the constant velocity exhibited in the absence of acceleration. The equation I chose for calculating metabolic rate was collected while individuals walked and ran at constant velocities. Using these equations for movements with accelerations underestimates metabolic rate (Seethapathi and Srinivasan 2015). By not considering how accelerations influence the total metabolic cost of a movement, these model predictions may slightly underestimate the actual metabolic cost of moving, especially when over shorter distances.

I estimated the metabolic cost of walking and running using previously published functions (Long and Srinivasan 2013). By estimating rather than directly measuring metabolic rate, I may have failed to capture differences due to the stature (Steudel-Numbers et al. 2007; Barnes et al. 2014) and/or body mass index (Browning et al. 2006; Peyrot et al. 2009) of the participants. However, if I assume that any error in metabolic cost is equal in direction between gaits (overestimation for both gaits or underestimation for both gaits), deviations in these estimations would likely have minimal consequences on the slope of how total metabolic energy predicts indifference.

If an individual did not have extensive experience with running, than it is possible that their ability to accurately represent the consequences of running is different when compared to an individual that regularly runs. I required participants to experience both walk and run options before making a decision with the intention that they would use this recent experience, rather than their past experiences prior to the experiment, when considering between each gait.

One final consideration is that participants always started and ended each trial at the same position. Because a common purpose of walking and running is to change the location of the animal, it is possible that the current protocol is not capturing an additional contributor towards the utility of a movement, net displacement. By having all trials result in a net displacement, I may see a change in how the relative influence of time and energy contribute to gait selection. A potential follow-up where trials do not start and end at the same position might help elucidate how net distance influences utility in gait selection.

## 4.6 Conclusion

These results provide evidence that when deciding between walking and running, humans make decisions according to a utility model that is more complex than solely minimizing metabolic energy or time. In response to different relative walking and running distances, participants made decisions that could be described according to a weighted combination of the metabolic and temporal costs tied to each gait, with an individual's tendency to minimize time influencing both how they established preferences between movements and subsequently, how those movements were executed.

# CHAPTER 5

# VIGOR OF REACHING MOVEMENTS: REWARD DISCOUNTS THE COST OF EFFORT

## 5.1 Abstract

Making a movement may be thought of as an economic decision in which one spends effort in order to acquire reward. Time discounts reward, which predicts that the magnitude of reward should affect movement vigor: we should move faster, spending greater effort, when there is greater reward at stake. Indeed, saccade peak velocities are greater and reaction-times are shorter when a target is paired with reward. Here, I focused on human reaching and asked whether movement kinematics were affected by expectation of reward. Participants made out-and-back reaching movements to one of four quadrants of a 14cm circle. During various periods of the experiment only one of the four quadrants was paired with reward, and the transition from reward to non-reward status of a quadrant occurred randomly. My experimental design minimized dependence of reward on accuracy, granting the participants wide latitude in self-selecting their movement speed, amplitude, and variability. When a quadrant was paired with reward, reaching movements had a shorter reaction-time, higher peak velocity, and greater amplitude. Despite this greater vigor, movements toward the rewarded quadrant suffered from less variability: both reaction-times and reach kinematics were less variable when there was expectation of reward. My results suggest that expectation of reward not only increases vigor of human reaching, but also decreases its variability.

## 5.2 Introduction

Imagine that you are sitting at your desk and the phone rings, but you don't recognize the number. You reach for the phone and answer to find it is an old friend. A few weeks later, they call again, but this time you recognize their number. Again you reach for the phone, excited to hear how they have been. Both scenarios require executing a reaching movement. Assuming the physical constraints of reaching (i.e., initial arm configuration, and end point goal) are identical; will the reaching movements be the same?

Early motor control models suggested that the kinematics of reaching movements may be described through minimizing costs such as endpoint variability (Harris and Wolpert 1998; van Beers et al. 2004) and energy consumption (Alexander 1997), but they commonly relied on simplifications that included fixed movement duration. Using this framework, movement kinematics were dictated by minimizing the combined weight of these costs (Burdet et al. 2001; Wang et al. 2016). If we apply these models to the example of answering the phone, they predict invariant kinematics in the two situations.

However, if we assume that the purpose of a movement is to acquire a more rewarding state, and that time discounts the value of reward, then movements carry a cost of time (Shadmehr et al. 2010). In this framework, slower movements diminish reward. As a result, reward justifies expenditure of effort to arrive at the goal earlier. Recent contributions have considered this idea by assigning a utility to each action that combines measures of weighted effort and reward (Niv et al. 2007; Haith et al. 2012; Rigoux and Guigon 2012; Berret and Jean 2016; Shadmehr et al. 2016). As a result, the

optimal level of vigor (defined as movement speed as a function of distance) is an interaction between optimizing two competing factors: the desire to get reward sooner, balanced via payment of higher effort. According to these models, when you recognize the phone number and expect a pleasant conversation, you might reach with greater vigor, spending more effort to answer the phone sooner.

Experimental evidence has demonstrated that animals produce faster movements when they expect reward. Non-human primates make faster saccadic eye movements toward targets paired with juice when compared to those same targets without juice (Takikawa et al. 2002). Similarly, humans make faster saccades when those movements are paired with explicit monetary rewards (Manohar et al. 2015, 2017) and also implicit reward, such as when the movement is directed towards a more informative target (Xu-Wilson et al. 2009). As humans deliberate between two rewarding stimuli, saccade velocity is faster when the eyes gaze at the preferred stimulus (Reppert et al. 2015). Furthermore, there is evidence that people who exhibit high temporal discounting in decision making also make more vigorous saccades, suggesting that even in the absence of explicit reward, the cost of time is greater in people who move more vigorously (Choi et al. 2014). Taken together, these experiments demonstrate that in the saccadic system, reward modulates vigor of movements.

The effect of reward on arm movements is less understood. In non-human animals, two reports have found that reward (juice/food) encouraged faster movements (Opris et al. 2011; Mosberger et al. 2016), while one report found no effect (Pasquereau et al. 2007). In humans, one report found that reaching was faster when the goal object had higher emotional valence (Esteves et al. 2016).

In the current study, I considered a reaching task to test whether reward discounted effort expenditure. Reward may modulate movement vigor, but increased vigor often coincides with reduced accuracy, which can reduce probability of reward. To address this potential confound, the task minimized dependence of reward on accuracy: rather than reaching to a point, participants reached to one of four quadrants. As a result, they had wide latitude in selecting movement velocity, trajectory, and amplitude. When the quadrant was paired with reward, the participants responded by increasing vigor: they reached sooner, with higher velocity, shorter duration, and greater amplitude. Interestingly, I also observed that increased vigor coincided with reduced variability, demonstrating that expectation of reward not only increased vigor, but also promoted consistency.

## 5.3 Methods

*Participants:*

Right-handed participants (n=20), naïve to the experiment (age=26 ± 4 years, mean ± SD, including 10 males and 10 females) gave written informed consent approved by the University of Colorado Institutional Review Board before participating in the experiment.

*Task:*

Participants were seated in a chair that limited trunk movement and held the handle of a robotic arm with their right hand (Interactive Motion Technologies Shoulder Elbow Robot). Using the handle, they controlled the location of a cursor that was

projected on an LCD monitor mounted in front of them at eye level (Figure 5.1A). The task began by placing the cursor (diameter=0.6cm) in the center of a home circle (diameter=0.9cm). After maintaining the cursor in the home circle for 150ms, the visual feedback of the home circle was extinguished and the computer simultaneously delivered an audiovisual cue to begin the trial. The auditory component of the cue was a short beep (50ms @110hz followed by 50ms @ 220hz) and the visual component was the illumination of a large red ring (radius=14cm) that was displayed with its center at the home circle. The ring included a marker that indicated the quadrant that served as the goal of the movement. The marker was placed in one of four possible locations ($45^o$, $135^o$, $225^o$ or $315^o$ from right horizontal) to specify the intended quadrant (Figure 5.1B,C). The sole criterion for success was that the cursor crossed the ring within a $100^o$ arc centered on the marker. As the reach began, visual feedback of the cursor was blanked. Once the invisible cursor crossed the outer ring within the quadrant, the outer ring changed color from red to gray indicating that the trial was completed and that the invisible cursor should be brought back to center. I refer to the location where the invisible cursor crossed the ring as crossing-point. There was no time limit to complete the trial, and no instructions were provided regarding a desired reach velocity. The cursor remained invisible until the return aspect of the movement when it entered a region within 9cm of the center of the home circle. At this point, the cursor and home circle were again made visible and a new trial could begin.
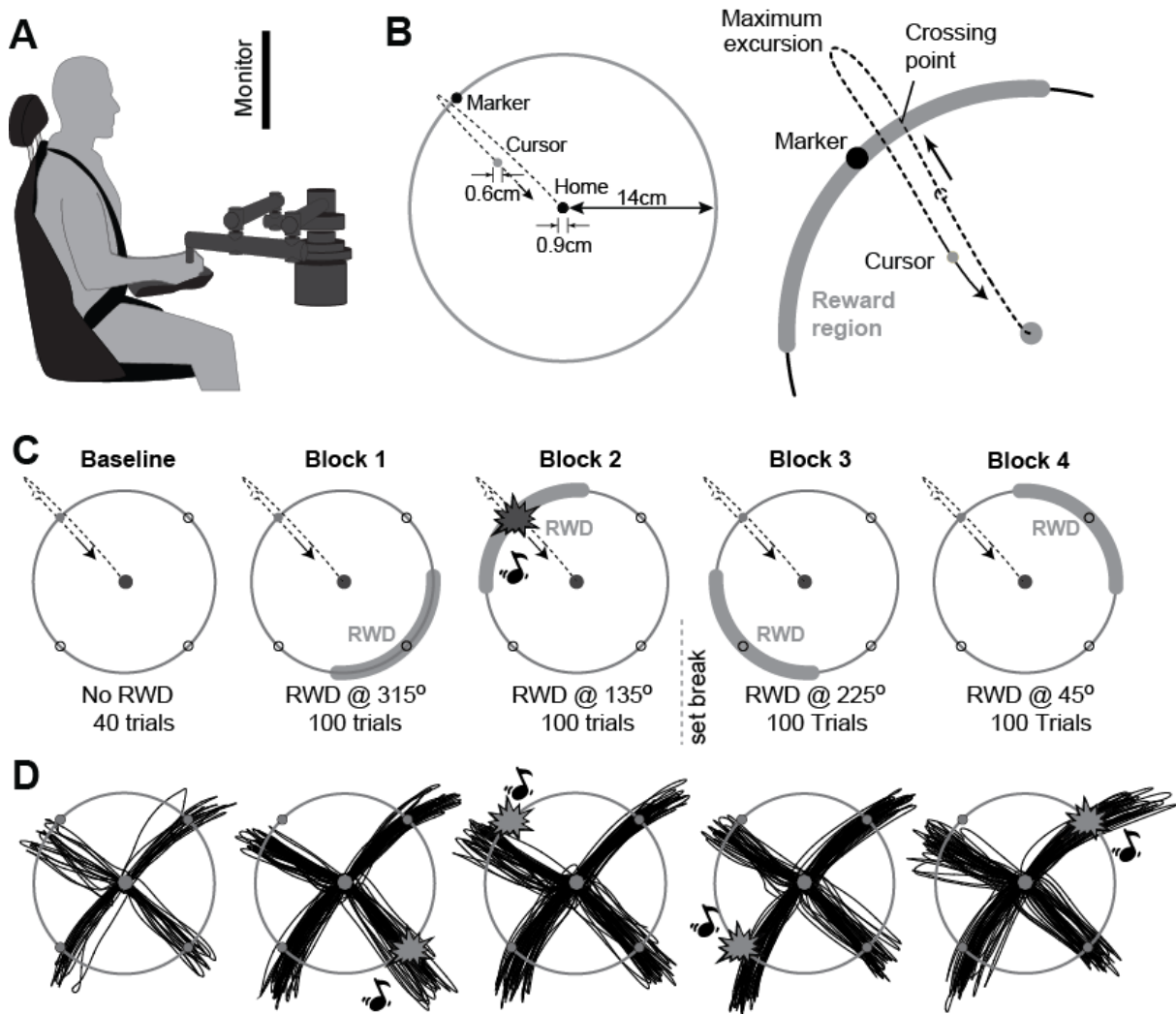
Figure 5.1 Experimental design. A) Set-up: Participants sat in a chair while grasping the handle of a robotic arm that controlled a cursor on a monitor located at eye level.  A shoulder harness was used to prevent movement of the trunk during the reaching task. B) Movement metrics: For each trial, participants completed out-and-back reaches to one of four alternating targets located 14cm from the home circle. Reaction-time, peak outward velocity, crossing point, maximum excursion, duration, and peak return velocity were recorded for each movement. C) Experimental protocol: The experiment consisted of a baseline period of 40 trials with no visual feedback or reward followed by four blocks of 100 trials. Each block had one target paired with a reward (RWD, indicated by quadrant with shaded gray region). The reward consisted of an exploding target, auditory stimulus, and four points. The order of rewarded blocks was randomized for each participant. D) Position data to each target for single participant (S3).

If the quadrant was associated with reward, and the invisible cursor crossed within the 100$^o$ reward region centered on the marker, the subjects experienced a pleasing sound (50ms @ 880hz followed by 50ms @ 3520hz) and a visual animation of the ring at the moment the invisible cursor passed the outer ring. The visual animation paired with reward consisted of the entire outer ring rapidly flashing yellow and then disappearing completely (transition from red to yellow to extinguished=50ms). The cursor remained invisible throughout the initial aspects of the return movement, after the reward was delivered, to guarantee that the visual qualities of reward were not obstructed by the visual feedback of the cursor. At completion of the trial, they also received 4 'points.' The cumulative points were displayed in the upper right corner of the monitor. Participants were not informed of the number of trials they would be performing, only that the experiment would take roughly one hour. Furthermore, each participant was informed that the compensation for participating in the study session ($15) was fixed and not contingent on the amount of points received from rewarded trials or any other measure of task performance.

I assumed that participants planned their reaching movements with the goal of wanting to maximize the chance of successfully completing the task and even in the absence of penalty, would reach towards the center of the cued quadrant (Trommershäuser et al. 2003). Previous research has demonstrated that on average, healthy people exhibited regular errors of up to 9±3$^o$ (mean ± SD) while holding a robotic arm and aiming to targets at 10cm (Smith and Shadmehr 2005). Based on this finding, the rewarded region was more than 5 times the expected error of reaching,

making it so that even in the presence of a persistent error, nearly all attempts should fall within the intended zone. Therefore, an important factor in the experiment design was an attempt to remove accuracy as one of the constraints typically associated with reward.

Upon arrival to the laboratory, all participants were seated and allowed ~40 trials to familiarize themselves with the robotic manipulandum. All familiarization trials occurred in the absence of reward and with full visual feedback of the cursor during both outward and return components of the movement. Upon conclusion of the familiarization phase, the experimental protocol consisted of a further 440 reaching trials. At the beginning of the protocol, the participants were informed they would no longer receive visual feedback of the cursor during their reach for the remainder of the experiment. They were also instructed that some trials would now be paired with a reward and that as long as they reached towards the indicated quadrant, they would receive the full reward. Importantly, participants were not told that a direction would be consistently rewarded in a block, nor were they made aware of the underlying block structure.

The first 40 experimental trials occurred in the absence of reward (baseline, Figure 5.1C). Following baseline, reward was introduced in one of the four directions (Block 1-4, Figure 5.1C). A reach was rewarded if it was within a $100^{o}$ arc centered on the marker and the direction was paired with reward. There was no feedback of any kind regarding accuracy of the movement: the only feedback was reward, and its only criterion was whether the reach was within the $100^{o}$ arc centered on the marker. The location of the reward zone was constant within each block of 100 consecutive trials (25 toward the rewarded location) and then changed to a new location for the next 100

trials. There was a short 30-second break between blocks 2 and 3. The order of rewarded quadrants was randomized for each participant. For 16 participants, trial-by-trial marker presentation within each block was randomized meaning that in blocks 1-4, there was on average a 25% chance that the next trial would be in the rewarded quadrant, even if the previous trial was also rewarded. The remaining 4 participants had a pseudo-randomized presentation of trials such that no rewards were presented consecutively. Participants never received instruction regarding the location of future reward trials, how reward location was distributed across blocks or when a new block with a new rewarded quadrant began.

*Data Analysis:*

Handle position and velocity were recorded at 200 Hz. Reaction-time was quantified as the time from the audiovisual start stimulus to movement onset. Movement onset was established via radial acceleration ($0.0001$ m/s$^2$) and radial velocity thresholds ($0.05$ m/s). Distance of the crossing-point referred to its distance relative to the marker, which was reported as the signed difference in degrees measured from the right horizontal, between the center of the quadrant and where the hand crossed the outer ring. Maximum excursion was calculated as the maximum Euclidean distance between the start marker and the cursor, measured over the course of the entire trial. Peak outward velocity was calculated as the maximum instantaneous radial velocity measured between movement onset and instant of maximum excursion. Movement duration was calculated as the elapsed time between when the cursor crossed a position threshold of 0.3cm and the crossing-point. Peak return velocity was calculated

as the maximum instantaneous radial velocity measured after the instant of maximum excursion.

Trials were removed from analysis if reaction-times was greater than 700ms. Across all participants, this accounted for exclusion of 0.43% of trials (43/8000 trials). In addition, I found that in only 0.03% of trials (2/8000 trials) the absolute value of the crossing-point distance of the reaching movement was off by more than $50^o$, signifying it fell outside the potential reward zone. Therefore, the large size of the reward region allowed for more than 99% of the trials to be potentially rewarding. Errant movements (absolute crossing-point distance of more than $50^o$) were excluded from analysis.

*Experimental design and statistical analysis:*

The location of the reward zone was reassigned after every 100 trials. In each period of 100 trials there were 25 movements towards each quadrant. To determine the effect of reward on the current movement, I measured how reaching was altered in the block when that movement was rewarded compared to blocks when that same action was not rewarded. Peak outward velocity, reaction-time, maximum excursion, duration, crossing-point, and peak return velocity were compared between the rewarded period (100 trials) and non-rewarded periods (300 trials) for each participant. To measure the effects of reward on movement variability, I calculated the variance of peak velocity, reaction-time, maximum excursion, duration and crossing-point for each quadrant when that quadrant was rewarded and compared it to the mean variance across the remaining three blocks when that same quadrant was not rewarded. I measured the effect of reward using a two-way repeated-measures analysis of variance (ANOVA)

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based on block number (discrete), whether the target was rewarded (binary), and a reward by block interaction. Differences in movements toward each quadrant were compared using a two-way repeated-measures ANOVA based on quadrant location, reward, and a reward by quadrant interaction. I used two-sided paired t-tests to compare movements towards rewarded quadrants and movement to non-rewarded quadrants in the trials immediately before and after a rewarded trial. Effects of repeating movements to the same quadrant were probed using a repeated-measures ANOVA based on whether the quadrant of the current movement was the same as the previous trial as well as whether the current quadrant was rewarded.

All statistical thresholds were conducted at a power of $\alpha$=0.05. All uncorrected p-values reaching statistical power were corrected for multiple comparisons using the Holm-Bonferroni method. ANOVAs and paired t-tests were corrected for a total of five comparisons, established based on the number of measured behavioral responses (peak velocity, reaction-time, crossing point, maximum excursion, and duration). Post-hoc comparisons on the effect of blocks and quadrants were corrected for a total of six comparisons. Descriptive statistics are reported as mean ± standard error.

## 5.4 Results

Participants (n=20) made a self-paced out-and-back reaching movement without visual feedback toward a marker that was positioned at 14cm, in one of four quadrants (Figure 5.1B). On each block of trials, only one of the quadrants (Figure 5.1C) was associated with reward (a pleasing sound and animation, as well as 4 points). Figure 5.1D illustrates reach trajectories for a single participant in various blocks. At the moment that

the unseen cursor crossed the 14cm ring, the mean absolute distance (for each participant) of the crossing point from the marker was 9.3±1.4 degrees. The sole criterion for success was that, on the outward component of the movement, the unseen cursor crossed within a $100^o$ arc centered on the marker. As a result, more than 99.9% of the movements across subjects crossed the outer ring within the potential reward zone. I asked whether expectation of reward altered movement preparation (reaction-time) and movement execution (velocity, extent, and variability).

*Effect of reward on reach kinematics*

I began my analysis by considering how the subjects reacted to presentation of the marker, which acted as the cue to reach to the quadrant. To quantify the effects of the marker appearing in a rewarded quadrant vs. non-reward quadrants, I computed the reaction-time distribution in each condition, and then computed a within-subject difference measure (Figure 5.2A). This difference measure was calculated for each individual as the probability density of reaction-time for all rewarded trials (bins=5ms) minus the probability density of all non-rewarded trials, with the difference measure then averaged across participants. It appeared that reward shifted the mode of the distribution earlier, and also reduced the variance of reaction-time distribution.

To quantify the within-subject change in the distribution of reaction-times, I constructed a delta-plot (Ridderinkhof et al. 2005), as shown in Figure 5.2D. For each participant and each condition (reward and non-reward trials), I ordered the reaction-times from shortest to longest and divided them into 20% quantiles. I computed the mean of each quantile, and then measured the within-subject change in the quantile

mean due to condition (reward minus non-reward trials). I found that for all quantiles, the change was negative, suggesting that reward reduced reaction-times in all range of responses. Furthermore, the negative slope indicated that the reaction-time distribution for reward was steeper (less variable) than the non-rewarded distribution, implying a reduced variance. In summary, reward appeared to have two effects on the reaction-time distribution: it shifted the mode of the distribution earlier, and it reduced the variance of the distribution.
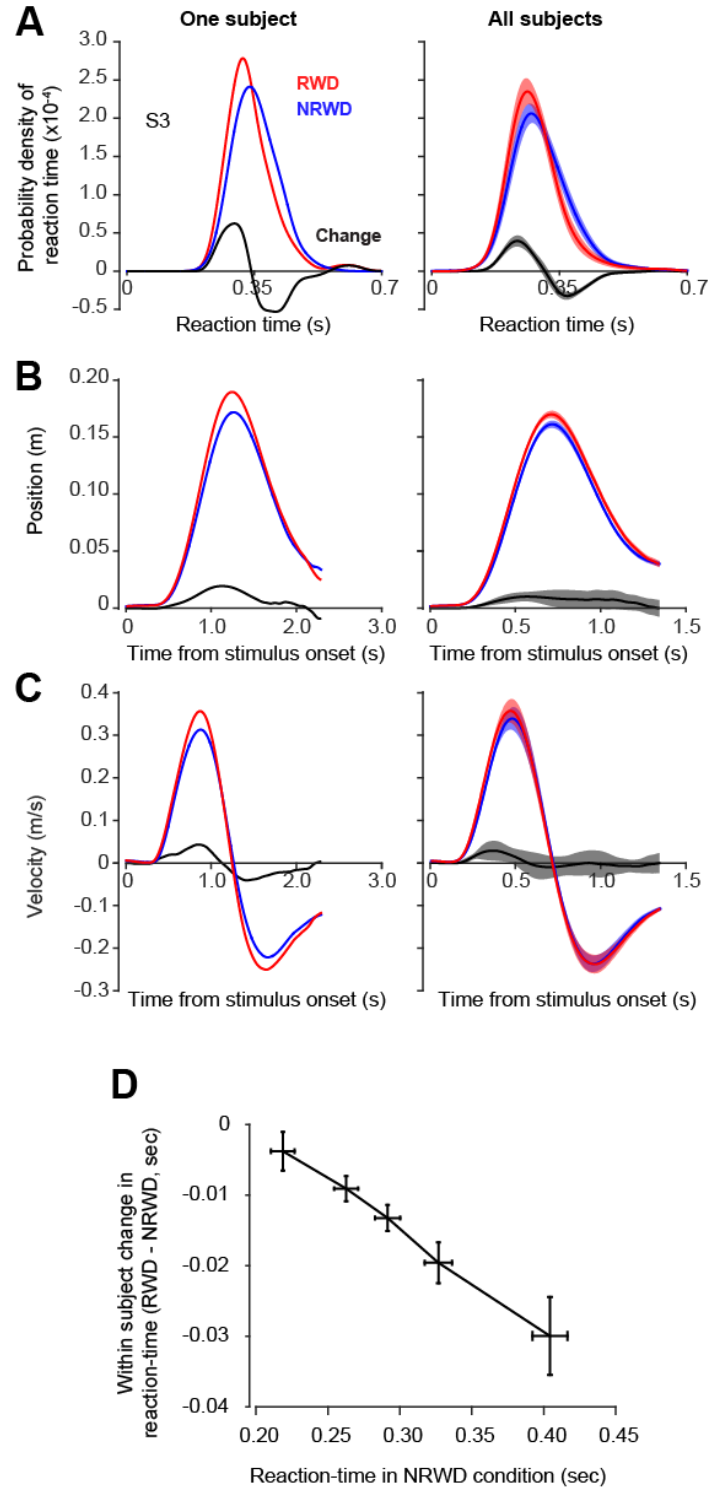
Figure 5.2 Movement characteristics. A) Probability distribution of reaction-time was estimated for each subject in each condition using a non-parametric approach (bin size is 5ms). The change in reaction-time is a within-subject measure. Mode of the reaction-time appeared to shift earlier and the variance appeared to decrease. B) Radial position trajectory and the change in radial position as a function of time. The hand appeared to

reach farther in the rewarded condition. C) Radial velocity and the change in radial velocity as a function of time. The hand appeared to reach faster in the rewarded condition. Due to the range of movement durations selected across participants, group averages are displayed up to the point of the shortest individual curve. Shaded regions represent ± SEM. D) Delta plot of reaction-time across 20% quantiles. For each subject, reaction-times in each condition were rank ordered and sorted into 20% quantiles. Values along the x-axis represent mean reaction time for NRWD at each quantile. Values along y-axis represent the change in the mean from RWD to NRWD condition. Negative values indicate that reward decreased reaction-times, and the negative slope suggests that reward reduced variance of reaction-times. Error bars represent ±SEM.

I next considered the effects of reward on the kinematics of the reach. I computed radial position and velocity of the hand as a function of time (Figures 5.2B and 5.2C) and found that in the rewarded condition, the subjects reached farther (peak of the red curve vs. blue curve, right column, Figure 5.2B), and reached faster (right column, Figure 5.2C).

To better characterize the effects of reward, I computed for each participant the change in various parameters of movement when a quadrant was paired with reward as compared to when the same quadrant was not paired with reward. In presence of reward, mean of the reaction-times decreased by 5.21±0.79% (15.20±0.10ms, $p<0.001$, Figure 5.3A), variance of the reaction-times decreased by an average of 24.0±6.32% ($p=0.006$, Figure 5.3B), outward peak velocity increased by 1.87±0.88% (0.78±0.01cm/s, $p=0.044$, Figure 5.3C), maximum excursion increased by 4.14±0.57% (0.73±0.01 cm, $p<0.001$, Figure 5.3D), and movement duration decreased by 4.56±1.05% (26.50±8.3ms, $p=0.002$, Figure 5.3E, duration refers to time to the crossing-point) (All p-values reflect corrections for multiple comparisons using Holm-Bonferroni method). In contrast, I found no effect of reward on mean crossing point ($p=0.613$). That is, the hand crossed the outer ring at a location (with respect to the

marker) that was on average unchanged with reward. In contrast, reward decreased crossing-point variance by an average of 10.10±4.18%. However, this effect was lost when corrected for multiple comparisons (uncorrected p=0.024, corrected p=0.096). I observed no effect of reward on the variance of peak velocity, maximum excursion, or duration (p's>0.05).
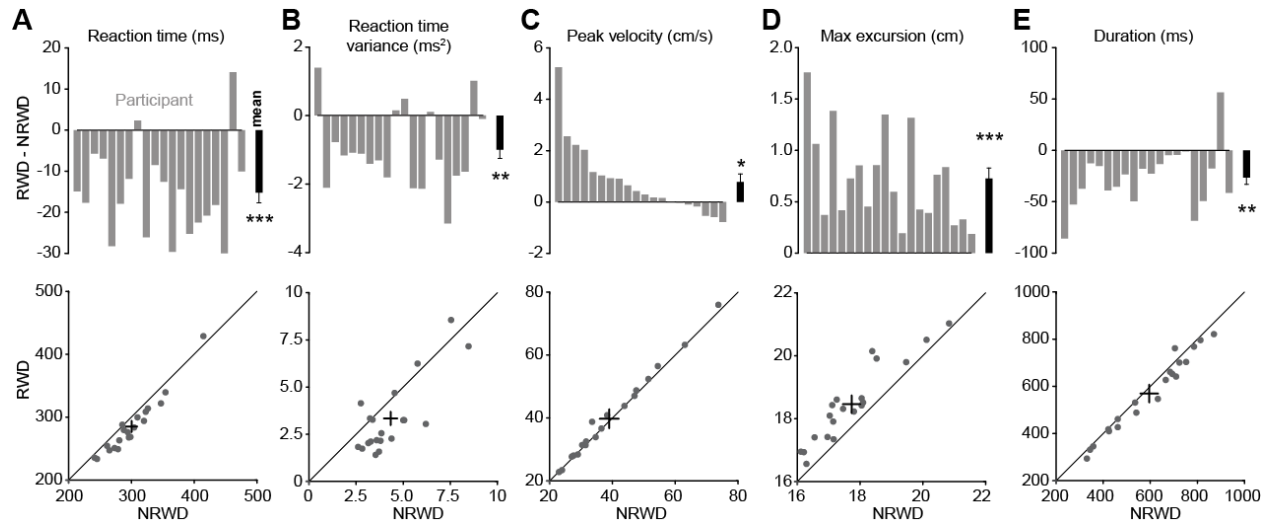


Figure 5.3 Within-subject measures on the effects of reward. Reward-dependent changes in A) mean of the reaction-times, B) variance of the reaction-times, C) peak velocity of the outward movement, D) maximum excursion, and E) duration of the outward movement. In bar plots, gray bars represent within-subject change and black bars represent group means ±SEM (*p<0.05, **p<0.01, ***p<0.001). Bar position reflects order of participant recruitment. Differences represent reward minus non-reward. In scatter plots, black dots represent individual participants and red lines represent group means ±SEM.

*Effect of reward across blocks*

Previous studies have noted that if subjects repeatedly made saccadic eye movements toward the same stimulus, the movements tended to become slower (Chen-Harris et al. 2008; Xu-Wilson et al. 2009). Here, I observed the opposite tendency: as the experiment progressed, participants increased the speed of their reaching movements (Figure 5.4A, RM-ANOVA, main effect of block, peak outward velocity

F(3,57)=8.748, p<0.001). Similarly, progression of the experiment coincided with a reduction in the mean reaction-time (Figure 5.4B, F(3,57)=10.500, p<0.001), as well as the variance of reaction-time (F(3,57)=4.692, p=0.005, Figure 5.4F). As the experiment progressed, duration of the reaching movements decreased (Figure 5.4D, F(3,57)=9.478, p<0.001). There were no changes across blocks for maximum excursion (Figure 5.4C, F(3,57)= 1.873, p=0.144); and no changes across blocks for mean crossing-point distance (Figure 5.4E, F(3,57)=0.662, p=0.579) or the variance in crossing-point distance (F(3,57)=0.356, p=0.785).

Importantly, the effect of reward on all movement parameters was consistent throughout the duration of the experiment (RM-ANOVA, block by reward interaction, peak outward velocity F(3,57)=0.509, p=0.678; reaction-time F(3,57)=1.344, p=0.269; maximum excursion F(3,57)=1.484, p=0.229; duration F(3,57)=0.515, p=0.674; crossing point F(3,57)=0.602, p=0.616). In summary, with the progression of the experiment, reach velocities tended to increase, and reaction-times tended to decrease. However, within-subject effects of reward remained consistent, influencing peak outward velocity (main effect of reward on peak velocity, F(1,19)=6.273, p=0.044, Figure 5.4A), mean reaction-time (F(1,19)=38.47, p<0.001, Figure 5.4B), maximum excursion (F(1,19)=51.77, p<0.001, Figure 5.4C), movement duration (F(1,19)=15.95, p=0.002, Figure 5.4D) and variance of reaction-time (F(1,19)=14.5, p=0.010, Figure 5.4F).
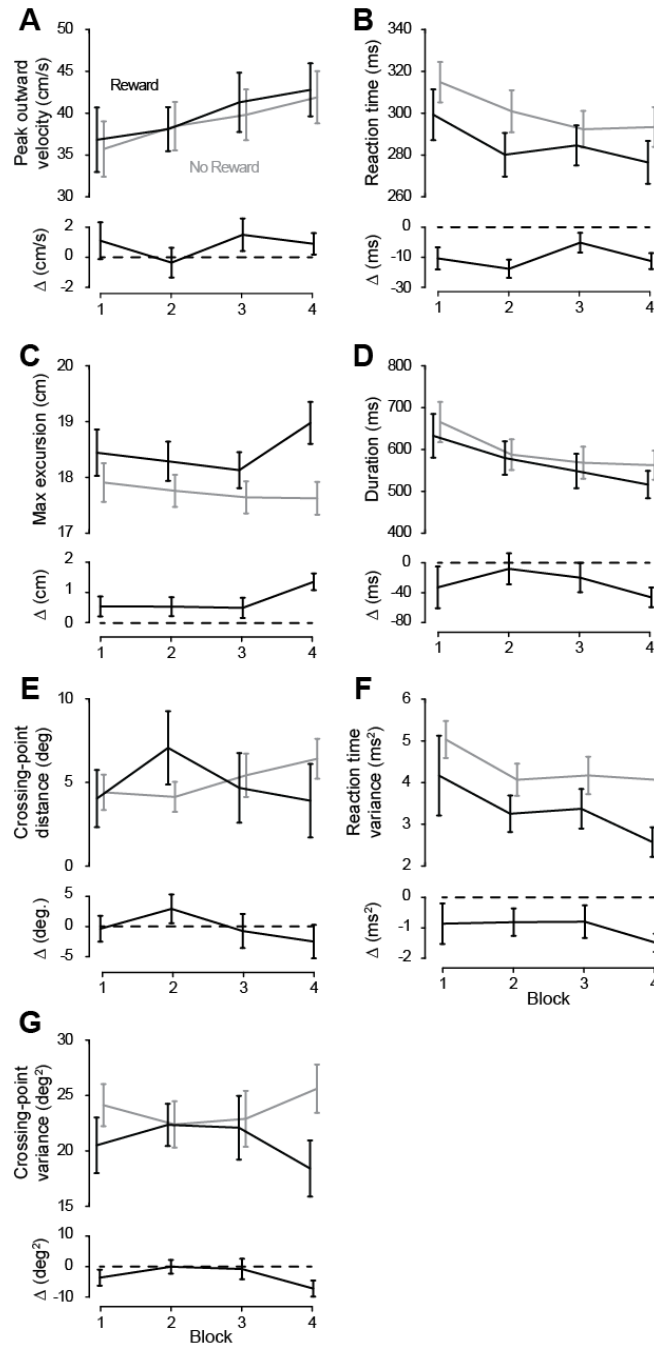
Figure 5.4 Effect of block number on reaching movements. Effect of block on A) peak outward velocity, B) reaction-time, C) maximum excursion, D) duration, E) crossing-point distance, F) reaction-time variance, and G) crossing-point variance. Red and black lines represent rewarded and non-rewarded trials, respectively. Bars denote means ± SEM. Graphs have been slightly offset horizontally to improve contrast. Results from post-hoc comparisons regarding the main effect of block are based on averages combining both rewarded and non-rewarded movements (* p<0.05, **p<0.01). Subset graphs represent within subject difference calculated as reward minus non-reward at each block.

*Effect of reward across quadrants*

Movements to each of the four quadrants required a unique combination of elbow and shoulder torques. This difference in joint torque combinations introduced the possibility that the amount of effort required for reaching was dependent on quadrant location (Schweighofer et al. 2015), and that reward may have affected movements differently at each location. Indeed, movement characteristics differed depending on which quadrant was cued. There was a main effect of quadrant on peak velocity $(F(3,57)=8.68$, $p<0.001)$, maximum excursion $(F(3,57)=9.43$, $p<0.001)$, and crossing point $(F(3,57)=42.12$, $p<0.001)$. Post-hoc comparisons indicated that peak velocity was slowest in quadrant 1 (Q1:36.70±2.84 m/s, Q2: 40.64±3.35 m/s, Q3:38.24±2.67 m/s, Q4: 41.07±3.49 m/s, $p_{1,2}=0.002$, $p_{1,3}=0.020$, $p_{1,4}=0.002$, $p_{2,3}=0.046$, $p_{2,4}=0.606$, $p_{3,4}=0.049$). Maximum excursion was shortest for movements towards quadrant 2 (Q1:18.15±0.32cm, Q2:17.02±0.30cm, Q3:18.21±0.30cm, Q4:18.29±0.37cm, $p_{1,2}<0.001$, $p_{1,3}=0.773$, $p_{1,4}=0.640$, $p_{2,3}<0.001$, $p_{2,4}=0.003$, $p_{3,4}=0.768$). Both crossing-point distance mean and variance were affected by quadrant location. Mean crossing-point distance was most positive (counter clockwise from quadrant center) in quadrant 3 and was most negative in quadrant 4 (Q1:7.66±1.46$^o$, Q2: 2.27±1.66$^o$, Q3:14.63±1.28$^o$, Q4:-4.37±0.94$^o$, $p_{1,2}=0.038$, $p_{1,3}<0.001$, $p_{1,4}<0.001$, $p_{2,3}<0.001$, $p_{2,4}=0.001$, $p_{3,4}<0.001$). Variance in crossing point was greater in quadrant 1 when compared to quadrants 3 and 4, with all other pairs being indistinguishable (Q1: 33.56±3.24$^o$, Q2:26.39±3.00$^o$, Q3:24.11±2.20$^o$, Q4:22.65±2.48$^o$, $p_{1,2}=0.099$, $p_{1,3}=0.022$, $p_{1,4}=0.022$, $p_{2,3}<0.532$, $p_{2,4}<0.213$, $p_{3,4}<0.565$). There was no effect of quadrant on reaction-time mean, reaction-time variance or duration.

While it was evident that the location of the quadrant affected a few of the movement kinematics, I found no interaction effects between reward and quadrant in any of the measured metrics (peak velocity $F_{(3,37)}=1.01$, $p=0.394$; reaction-time $F_{(3,37)}=0.23$, $p=0.878$; maximum excursion $F_{(3,37)}=0.77$, $p=0.514$, duration $F_{(3,37)}=0.13$, $p=0.942$; crossing point $F_{(3,37)}=1.77$, $p=0.163$). In summary, the location of the quadrant influenced movement vigor, but the effect of reward was quadrant independent.

*Effect of temporal proximity to a rewarding movement*

If expectation of reward affected movement vigor, what was the temporal window of these effects? Did increased vigor due to reward on one trial influence vigor of the subsequent movements? To explore these questions, I compared movements to the rewarded quadrant with the movements that were made immediately before and after, toward other (non-rewarded) quadrants (Figure 5.5). I found that in comparison to the rewarded trial, the immediately preceding non-rewarded trial had reduced outward peak velocity (two sided paired t-test, reward trial compared to previous trial, $p=0.041$), increased reaction-time ($p<0.001$), reduced excursion ($p<0.001$), and increased duration ($p=0.037$). Similarly, the non-rewarded trial immediately following the rewarded trial exhibited reduced peak outward velocity (two sided paired t-test, reward trial compared to subsequent trial, $p=0.006$), increased reaction-time ($p<0.001$), reduced excursion ($p<0.001$), and increased duration ($p<0.001$). The average crossing point was unchanged between reward and surrounding non-rewarded trials ($p$'s$>0.05$).

I next considered the effects of reward on movement variance and found that reaction-time variance was lower in the rewarded trial when compared to the preceding non-rewarded trial (p=0.030). However, this same comparison in variance for crossing point resulted in indistinguishable differences (p=0.126). Trials immediately following reward exhibited increased variance in both reaction-time and crossing point ($p_{rxn}$=0.019, $p_{cross}$=0.024).

Therefore, increased vigor and reduced variability were specific to the rewarding target and were not shared with temporally nearby movements to non-rewarding quadrants.
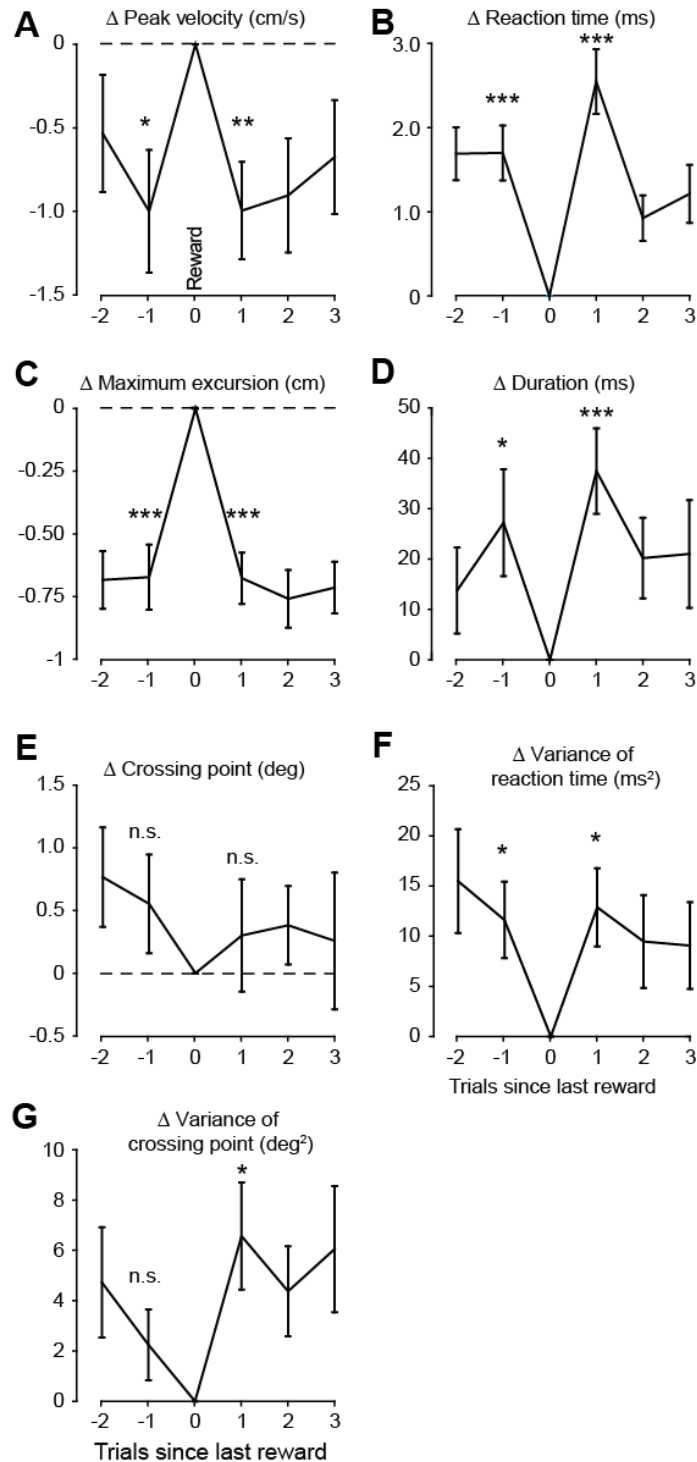
Figure 5.5 Trial to trial effect of reward. Change in A) peak outward velocity, B) reaction-time, C) maximum excursion, D) duration, E) crossing-point distance, F) variance of reaction-time, and G) variance of crossing-point distance as a result of reward on subsequent and preceding non-rewarded targets (* p<0.05, **p<0.01, ***p<0.001 compared to RWD, n.s.=not significant). All reported values are relative to the rewarded trial. Bars denote means ± SEM.

*Effect of spatial proximity to a rewarding movement*

I tested whether spatial proximity to the rewarded quadrant influenced the vigor of the movements towards adjacent and opposite non-rewarded quadrants. I measured kinematics of non-rewarded movements (reaction-time, peak velocity, maximum excursion, and crossing point) when a quadrant was adjacent to reward and compared it to the kinematics when that same quadrant was opposite the reward quadrant. I found no difference between any measures for movements adjacent and opposite to the rewarded quadrant (p's>0.05).

The large 100-degree arc for each quadrant meant large deviations from the center would still result in a successfully completed trial. When a rewarded quadrant was adjacent to a cued non-rewarded quadrant, it was possible that the rewarded quadrant could act as a distractor (or attractor) and influence the crossing point for the non-rewarded movement either towards or away from the direction of the rewarded quadrant. To test for the presence of a reward influenced bias, I measured crossing point distance for each target when the clockwise quadrant was rewarded and compared it to the crossing point distance when the counter-clockwise quadrant was rewarded. For example, when testing for the effect of reward proximity in quadrant 1, I averaged crossing point distance in non-rewarded movements to quadrant 1 when quadrant 3 was rewarded and compared it to crossing-point distance in non-rewarded movements to quadrant 1 when quadrant 4 was rewarded. Looking at movements to each quadrant independently, I found that there were no differences in crossing-point distances in quadrant 1 (reward in quadrant 3 ($R_3$)=7.51±1.43, reward in quadrant 4 ($R_4$)=8.37±1.58, p=0.316), in quadrant 2 ($R_3$=14.57±1.53, $R_4$=14.95±1.42, p=0.714), in

quadrant 3 ($R_1$=2.42±1.77, $R_2$=1.79±1.87, p=0.367), or quadrant 4 ($R_1$ = -4.70±0.97, $R_2$=-4.58±0.98, p=0.855).

In summary, I found that the effects of reward were both temporally and spatially specific to the quadrant that was rewarded.


*Effects of repeating movements to the same quadrant within a block*

Movement history appears to influence arm choice by discounting effort when movements are repeated with the same arm as in preceding trials (Schweighofer et al. 2015). In the current paradigm, there were several instances in which subsequent movements were cued to the same quadrant (~25% of the time). If we assume that reward discounts effort, then the observed effects of reward may be enhanced by movements being repeated. I found that repeating consecutive trials to the same quadrant increased peak velocity (main effect of repetition, peak velocity ($F_{(1,15)}$=18.47, p=0.016), increased reaction-time ($F_{(1,15)}$=15.76, p=0.004), increased excursion ($F_{(1,15)}$=25.78, p<0.001), reduced duration ($F_{(1,15)}$=9.692, p=0.014), and increased reaction-time variance ($F_{(1,15)}$=19.08, p=0.003), but not crossing point mean or variance.

My main question was whether presence of reward affected these changes. Indeed, I found that the effects of repetition on reaction-time, maximum excursion and duration depended on whether the movements were rewarded or not (reward by repetition interaction, reaction-time $F_{(1,15)}$=25.00, p=0.001; maximum excursion $F_{(1,15)}$=10.49, p=0.010; duration $F_{(1,15)}$=13.36, p=0.008; crossing point $F_{(1,15)}$= 22.05, p<0.001). In the presence of reward, repetition further increased maximum

excursion (0.93±0.20cm, p=0.001), and further reduced duration (56±13ms, p=0.002). Repetition of rewarded trials also increased crossing-point distance (1.64±0.44$^{o}$, p=0.006). There was no effect of repetition in rewarded trials for peak velocity, reaction time, reaction time variance, or crossing-point variance (p's>0.05). In the absence of reward, repetition led to longer reaction-times (30±6ms, p<0.001), greater maximum excursion (0.32±0.10cm, p=0.015), and increased reaction-time variance (2±0.5ms$^{2}$, p=0.001). Therefore, repetition of reward led to faster and larger movements.

*Effect of reward across segments of a single reaching movement*

The auditory and visual cues that indicated success were delivered as the unseen hand crossed the outer circle. However, the movement continued to a self-selected turnaround point, and then the subject brought their hand back to center. Therefore, the trial was composed of two phases of movement (out and back). During rewarded trials, the visual target explosion and auditory beep were delivered at the crossing point of the outward movement. That is, acquisition of reward was associated with only the outward phase, not the return phase. Did reward modulate vigor during both movement phases?

I found that the outward peak velocity was on average 5.49±0.88 cm/s (15.59%±2.17%) faster than the peak return velocity (two-sided paired t-test, p<0.001). While reward produced an increase in the peak outward velocity of 0.78±0.01cm/s (1.87±0.88%, p=0.044, Figure 5.3A), the return velocity of the same movement was indistinguishable between rewarded and non-rewarded trials (rewarded=33.92±2.47 cm/s, non-rewarded=33.60±2.39 cm/s, ANOVA, main effect of reward, $F_{(1,19)}=1.273$,

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p=0.273). In summary, the effect of reward was specific to the outward phase of the movement (the phase preceding acquisition of reward), and not present in the return phase after reward was acquired.

## 5.5 Discussion

Reaching movements paired with reward exhibited reduced reaction-time, higher peak velocity, shorter duration, and larger excursion. Despite increased vigor, movement variability remained largely intact, and in some cases was reduced. These changes were specific to the rewarded trials, with little transfer to temporally or spatially nearby non-rewarded movements.

*Reward led to higher vigor*

Increases in amplitude and speed of a reaching movement produce increases in the metabolic cost of that movement (Shadmehr et al. 2016). If I view metabolic cost as a proxy for effort, my results suggest that subjects were willing to expend more effort when the goal was paired with reward: reaching in rewarding quadrants not only produced a 4% decrease in duration, but also a 4% increase in excursion.

Why do subjects reach further in the rewarded trials? A potential explanation is to increase probability of reward. All movements were rapid, out-and-back shooting movements, but reward was only acquired if the invisible cursor crossed the arc. I found no effect of reward on the proportion of trials where the reach turned around prematurely (1.90±0.53% for reward compared to 3.12±0.61% for no reward, p=0.099).

However, it is possible that subjects reached further to minimize the possibility, albeit unlikely, of turning around before reaching the arc, thus missing the reward.

My results add to the significant literature demonstrating that movements that are paired with reward result in reduced reaction-times (Kawagoe et al. 1998; Watanabe and Hikosaka 2005; Bendiksby and Platt 2006; Milstein and Dorris 2007; Opris et al. 2011; Mosberger et al. 2016). However, I observed that in addition to reduction in the mean of the reaction-time, reward also decreased the variance of the distribution, a fact that has not been noted before.

Reaction-time is commonly explained using drift diffusion models (Ratcliff and Rouder 1998) in which evidence towards a decision accumulates until it reaches a threshold. The rate of evidence accumulation is influenced by properties of the stimulus, as well as attention invested towards that stimulus (Milstein and Dorris 2007). In the current paradigm there were no reward specific environmental cues, suggesting that the strength of the stimulus that beckoned the movement did not affect the rate variable. However, attention may be selective towards rewarded targets (Milstein and Dorris 2007). In my experiment, reward could lead to greater attention towards those quadrants and away from non-rewarded quadrants, allowing for faster accumulation of evidence to initiate movement toward reward.

The current task involved participants learning to control a robotic manipulandum to move an invisible cursor through alternating quadrants around a central point. In a majority of the trials, the only feedback of the movement was the outer ring changing color from red to gray. In a smaller fraction of trials, the movement outcome was increased with the outer ring flashing yellow while being paired with a short auditory

stimulus. By altering the feedback associated with completing each reach, I may have altered the relative sense of agency or contingency between rewarded and non-rewarded movements (Elsner and Hommel 2004; Behne et al. 2008). In an effort to probe how contingency effects movement performance, Karsh and Eitam (2015) had participants press one of several keys on a keyboard in response to cues. In a proportion of those trials, irrespective of the button selected, an added visual stimulus was displayed indicating that the trial was successfully completed. The researchers then estimated each participant's agency as a function of the number of trials paired with the stimulus and found that an increased sense of agency correlated with decreased reaction-times. Manohar et al. (2017) report that the presence of reward increases peak velocity for saccades, with the greatest effects observed when reward was highly contingent on saccade velocity (higher velocity=greater reward) rather than when reward was not contingent on velocity (reward delivered independent of velocity). The reward in the current study had minimal contingency with the reaching movement. Participants only needed to reach to the correct quadrant to receive reward. However, the additional audio-visual stimuli in movements paired with reward may have indirectly influenced the participants' sense of contingency, contributing to the observation that reward decreased reaction-time.

*A computational model of reaction-time and vigor*

A single computational framework may account for the observation that reward produced both a reduction in reaction-time, and an increase in movement vigor. Let us express utility of a reaching movement as reward minus effort, divided by duration of

that movement. This utility is the net rate of reward, where metabolic cost serves as a proxy for effort (Shadmehr et al. 2016):

$$J = \frac{\alpha - aT - bd/T^2}{T}$$
[ 5.1 ]

In this expression, $\alpha$ represents the reward associated with the outcome of a successful movement. In the above model, $\alpha$ is represented in units of energy, specifically joules. Movement duration is represented as *T*, and movement distance as *d*. The remaining variables are constants that reflect the metabolic cost of reaching across a range of movement speeds and distances. Given the objective of maximizing net rate of reward, the optimum movement vigor is defined via duration $T^*$ :

$$T^* = \left( \frac{3bd}{\alpha} \right)^{1/2}$$
[ 5.2 ]

The above expression implies that reward decreases the optimum movement duration, resulting in increased vigor. At the optimum duration, the resulting utility of the movement is:

$$J^* = \frac{2\alpha^{3/2}}{3\sqrt{3bd}}$$
[ 5.3 ]

This implies that as reward increases, the utility of that option increases. During reaction-time, decision-making proceeds by integrating to threshold a random variable. If that random variable has a mean that is proportional to the rate specified by the utility of that action [eq. 5.3], then the rate of rise increases as reward increases, producing an earlier reaction-time. As a result, a utility that is defined as the rate of net reward, where effort is the metabolic cost of the action, can account for both the effect of reward on vigor, and the effect of reward on reaction-time.

*Increase in vigor does not increase variability*

In general, found that reward reduced the variability of reaction-time. Works by Takikawa et al. (2002), Manohar et al. (2015), and Manohar et al. (2017) examined saccades and found that reward led to both an increase in vigor while reducing endpoint variability. In reaching, Nikooyan et al. (2015) observed that, in an adaptation task, the addition of reward feedback led to greater reductions in reach endpoint variability compared with visual feedback alone. In addition, Pekny et al. (2015) found that reward probability altered reach variability, with movements occurring under high probability of reward being less variable than movements under low probability. Further, they found that reward-dependent control of variability was impaired in Parkinson's disease, suggesting a role for the basal ganglia.

A central source of variability may be the neural activity during the delay period when the movement is being planned. Churchland et al. (2007) noted that trial-to-trial variability in the activity of cells in the primary motor cortex and premotor cortex during the delay period accounted for roughly half of the variability in reach velocity. Although the effect of reward on the delay period activity of reach-related neurons is not well understood, pairing of a stimulus with reward tends to increase the delay period activity of neurons that direct a saccade toward that stimulus (Ikeda and Hikosaka 2003), an effect that is similar to changes associated with increased spatial attention (Ignashchenkova et al. 2004). Based on this, it is possible that the reward related changes in reach variability may be associated with preferential allocation of spatial attention.

*Neural correlates in reward-dependent modulation of vigor*

Natural variations in dopamine levels can predict the amount of effort an individual will exert for reward (Wardle et al. 2011). In Parkinson's disease, dopamine levels deteriorate, slowing movement (bradykinesia) (Hallett and Khoshbin 1980). This symptom is traditionally believed to be due to increased signal dependent noise in the motor system (Montgomery and Nuessen 1990; Phillips et al. 1994). An alternative or perhaps complementary explanation of bradykinesia is that dopamine is essential in establishing vigor, with the pathology leading to a general decrease in motivation to move (Mazzoni et al. 2007; Kojovic et al. 2014; Salimpour et al. 2015) as well as decreased ability to adjust movements in response to changing reward landscapes (Schmidt et al. 2008b; Kojovic et al. 2014; Pekny et al. 2015). Including individuals with Parkinsonian symptoms in the current paradigm, with its low consequences on accuracy, may provide a promising platform for helping to further elucidate the role of dopamine in modulating both the vigor and variability of our movements.

*Limitations*

My protocol only considered two conditions: reward vs. no reward. As a result, I did not quantify or modulate the value of reward. Adding auditory and visual reward coincided with an increase in reaching velocity of around 2%. Xu-Wilson et al. (2009) reported a 1% increase in saccade velocity towards images of human faces compared to other images. Non-human primates exhibit much greater changes in saccade velocity to obtain juice rewards (~25%) (Kawagoe et al. 1998; Takikawa et al. 2002). This difference may be due to reward modality. In my study, as well as the study by Xu-

Wilson et al. (2009), reward had no explicit utility when compared to the caloric rewards in the non-human primate studies.

Quantifying reward based on its metabolic/energetic content predicts when starlings choose to walk and fly (Bautista et al. 2001). Studies on humans have used monetary rewards to study movement decisions under uncertainty (O'Brien and Ahmed 2015, 2016), however, these rewards exhibit significant distortions from their actual value which vary across individuals (Kahneman and Tversky 1979). Other intrinsic reward mediums are more difficult to quantify, such as the value of different images (Xu-Wilson et al. 2009). Furthermore, little is understood about how these intrinsic rewards compare to other extrinsic rewards such as food or money.

One potential method of developing a universal currency for reward may be through understanding how different rewards affect neural activity, specifically between regions of the prefrontal cortex and dopaminergic striatum (Levy and Glimcher 2011, 2012). This foundation has been considered in a model of motor control that predicts movement responses (lever presses) based on levels of dopamine (Niv et al. 2007). The model advances the role of environment by considering reward's influence on dopamine activity on both a phasic (quality of individual rewards) and tonic level (rate of reward). Understanding how the dopaminergic midbrain responds to reward may prove essential in explaining movement preference both across and within populations.

My experiment did not control inter-trial intervals. The only temporal constraint between trials was a short 150ms period of time when the cursor was held in the start circle. Other than this delay, the pace of the experiment was limited only by how quickly participants completed their trials. Research focusing on inter-trial intervals suggests

that it is not just reward quality, but also reward rate that alters movements (Niv et al. 2007; Haith et al. 2012). Not controlling reward rate, in principle, may explain the observed increase in vigor as the experiment progressed.

## 5.6 Conclusion

Humans reacted with shorter latency, and produced faster and longer reaching movements when anticipating reward. In addition to modulating vigor, reward also led to more consistent movements, reducing the variance of the reaction-times, when compared to similar, non-rewarded movements. These results support the idea that vigor is not optimized solely by minimizing effort costs or error, but instead depends on a utility where reward discounts effort.

# CHAPTER 6

# AGING REDUCES SENSITIVITY TO REWARD
# IN A REACHING TASK

## 6.1 Abstract

The vigor with which we move depends on both the opportunity for reward and the effort we are willing to spend to obtain that reward. In this chapter, I sought to understand how effort and reward influence reach vigor in older and younger adults. Aging is accompanied by both a decreased sensitivity to reward and potentially an increased expenditure of effort. These changes suggest that when making reaching movements, older adults will be less likely to alter vigor in response to reward. I objectively quantified effort expenditure during reaching in young and older adults and measured their willingness to adjust the amount of effort exerted in a changing reward landscape. In response to added reward, older adults, like young adults, initiated their movements earlier and more consistently. However, when executing these movements, older adults, unlike young, did not adjust their velocity or extent. I sought to explore whether an elevated cost of effort could explain why older adults did not alter movement execution. Effort, quantified objectively as metabolic cost, was measured as older and young adults reached across a range of distances and durations. I found that across the tested movement constraints, metabolic cost was indistinguishable between age groups. The results of these two experiments together suggest that the reluctance of older adults to adjust the execution of their reaching movements in response to increasing reward cannot be explained by an increase in objective effort, but rather appears more likely due to a decreased sensitivity to the properties of the rewarding stimulus itself.

## 6.2 Introduction

The manner in which an individual moves about their environment can inform us about how they value that environment. In response to changing reward landscapes, humans and other animals adjust the vigor of their movements (defined as the speed as a function of duration), even when doing so has no impact on reward contingency (Manohar et al. 2017; Summerside et al. 2018).

When making saccadic eye movements towards targets paired with a juice reward, non-human primates increase the vigor of their saccades when compared to similar movements in the absence of reward (Kawagoe et al. 1998; Takikawa et al. 2002). Similarly, humans saccade more vigorously towards informative images (pictures of faces) when compared to images of static (Xu-Wilson et al. 2009). In situations where individuals are asked to weigh alternative rewards, the vigor of their saccades can predict reward preference, with this effect growing based on the relative difference in value to the alternative (Reppert et al. 2015). These reward-induced adjustments in movement vigor have also been reported in other movements including reaching (Opris et al. 2011; Summerside et al. 2018) and locomotion (Dumont et al. 1998; Stevens et al. 2005).

The dynamics of movement vigor have previously been explained based on the interactions of a movement's costs (mainly variability, effort and temporal costs) and benefits (Haith et al. 2012; Rigoux and Guigon 2012; Shadmehr et al. 2016). Changing the relative weighting of these contributing variables alters the predictions on how an individual establishes the vigor of their movements (Shadmehr et al. 2010).

The gradual decline in movement vigor is a distinctive phenomenon of healthy aging. Older adults walk at a slower preferred velocity (Waters et al. 1988; Laufer 2005), make slower saccades (Irving et al. 2006; Dowiasch et al. 2015), and reach at slower velocities (Ketcham et al. 2002; Kozak et al. 2003). These observations have been independently explained as a result of decreased reward sensitivity and increased effort costs. However, we lack a clear understanding of how aging influences the way these costs and benefits interact when establishing vigor.

The brain's ability to accurately predict the value of an upcoming reward depends on the integrity of the dopaminergic midbrain (Schultz et al. 1997). Individuals with deficits to this region exhibit a diminished willingness to exert effort for increasing reward (Schmidt et al. 2008b; Chong et al. 2015). The function of the dopaminergic system declines in healthy aging, showing a diminished response to changing reward when compared to younger adults (Dreher et al. 2008; Eppinger et al. 2011). This decrease in reward sensitivity is one explanation for why older adults may make slower saccades (Shadmehr et al. 2010).

An alternative, though not exclusive explanation, is that effort costs may be elevated in older adults; thus the cost of increased vigor may offset the reward to be obtained. Indeed, across a range of natural walking speeds, older adults exhibit an increase in metabolic rate when compared to younger adults (Waters et al. 1988; Martin et al. 1992; Ortega et al. 2014). Greater effort costs can be explained through a combined decrease in efficiency of the mitochondria and contractile elements of muscle (Conley Kevin E. et al. 2012) as well as increased coactivation of antagonist muscle groups (Ortega and Farley 2015). Less is understood about how metabolic cost

changes across age when executing reaching movements. One study found that when performing hand cycle ergometry, older and younger adults exhibited similar metabolic responses to increasing mechanical output when controlling for muscle mass (Aminoff et al. 1996). When learning high energy coordinated reaching movements, older adults were able to reduce metabolic cost to a level similar to younger adults, however they maintained an elevated heart rate (Sparrow et al. 2005). Huang and Ahmed (2013) compared how young and older adults decreased metabolic cost while adapting to a dynamic force field. They reported that older adults exhibited lower overall compensation for the perturbation, however, their decrease in metabolic cost was similar to that of the younger adult group. To my knowledge, there is yet no report describing how age influences the metabolic cost of reaching across increasing distances and durations.

Here, I designed a pair of experiments intended to directly measure how increasing age affects the relative contributions of reward and effort when selecting movement vigor in a common task: reaching. First, I measured how older adults modulated vigor when making unconstrained reaching movements in a dynamic reward environment and compared those behaviors to the responses of younger adults in the same task. Next, I measured the effort, quantified objectively as metabolic cost, required to reach across a range of constrained distances and durations. Together these studies allowed me to ask whether differences in metabolic cost across velocities could explain an individual's inclination to increase vigor in response to heightened reward, specifically when comparing young and older adults. I hypothesized that older individuals would exhibit weaker reward-based modulation of vigor as a combined result

of a decreased sensitivity to the qualities of the reward itself and an increased cost of effort needed to increase vigor.

## 6.3 Methods

*Participants*

A total of 20 older adults (72±6 years, 10F, 10M) participated in experiment 1. Twelve older adults participated in experiment 2 (75±8 years, 6F, 6M). Participants were naïve to the experiment and gave written informed consent approved by the University of Colorado Boulder Institutional Review Board before participating in this protocol. All participants reported being primarily right-handed (Oldfield 1971) and reported no issues regarding their physical or mental health. Additionally, all older adults were deemed fully mobile as evident in earning the maximum score when performing a short physical performance battery (Guralnik et al. 1994). Young adult data for experiment 1 (26±4 years, 10M, 10F) has been reported previously in Summerside et al. (2018) and for experiment 2 (27±4 years, 8F, 7M) in Shadmehr et al. (2016).

*Experiment 1: Effect of reward on reaching vigor*

Participants sat in a chair designed to limit trunk movement and grasped the handle of a robotic arm using their right hand (Interactive Motion Technologies Shoulder Elbow Robot). The robotic handle operated similarly to a computer mouse, where movements along the horizontal plane controlled the position of a virtual cursor projected on a vertically positioned LCD monitor located at eye level (Figure 6.1A). A trial began with a small green circular home target (diameter=0.9cm) appearing in the

center of the screen. Participants moved the cursor (diameter=0.6cm) to overlap with the home target. After overlapping for a brief 150ms, the home circle vanished, a quick audio stimulus was delivered (50ms @110hz followed by 50ms @ 220hz), and a larger red outer circle appeared (diameter=14cm) with its center the same as the home target. The outer ring included a small indicator located at one of four alternating locations ($45^o$, $135^o$, $225^o$ or $315^o$ from right horizontal). The goal of the task was to move the cursor through the outer ring while staying within the quadrant containing the indicator (Figure 6.1B). Once passing the outer ring, the outer ring changed color from red to gray, signaling to the participant that they should return the cursor to the center. When the cursor returned within 9cm of the center, the home target was re-illuminated to allow the next trial could begin.

In a minority of the trials a quadrant would be paired with a reward. The only requirement for receiving the reward was that the cursor crossed the 100-degree region centered on the quadrant indicator. This large region was intended to remove any differences in movement kinematics related to movement variability.

The qualities of the reward stimulus consisted of a pleasing sound (50ms @880hz followed by 50ms @ 3520hz) and a visual animation of the outer ring (ring flashed yellow for 50ms and disappeared), both simultaneously delivered when the cursor crossed the outer ring. At the end of a rewarded trial, participants received 4 points, with the total accumulated points displayed on the upper right corner of the monitor.

Importantly, participants were instructed only to reach in the direction of the indicated quadrant and were informed that nothing they did beyond that would change

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the quantity or quality of the reward. As long as they completed the trial in the indicated quadrant and that trial was rewarded, they would receive the full reward. If participants inquired about whether they needed to perform under any time or kinematic constraints, they were told that there was no wrong way to perform the movement and to simply reach in a manner that felt natural for them. The participants were unaware of the number of trials they would be completing, only to expect the experiment to last one hour. Each participant was compensated $15 for their time with this amount being independent of any aspect of their performance in the task.

Experiment 1 began with a familiarization protocol consisting of a single block of 40 trials (10 trials to each quadrant). During these trials, participants were able to familiarize themselves with the task as well as adjust the position of the chair to ensure all four quadrants could be comfortably accessed.

The experimental protocol came after familiarization and consisted of a baseline block of 40 trials (Figure 6.1C, 10 trials/quadrant) followed by four experimental blocks of 100 trials (25 trials/quadrant). At the start of the experimental protocol, the participants were informed that they would no longer be receiving visual feedback of their cursor when reaching. They were also told that targets would now be occasionally rewarded and that as long as they reached in the indicated quadrant, they would receive the full reward.

At the start of each trial, visual feedback of the cursor was removed. The cursor re-appeared during the return movement once arriving within 9cm of the home target. There was no reward tied to any quadrant during the baseline block. In each of the

experimental blocks, a single quadrant was consistently rewarded, with the location of the reward changing at the beginning of each new block.

The presentation of quadrants was completely random within each experimental block. This means that there was a 25% probability that the next trial would be in the rewarded quadrant. No participants were ever explicitly informed about when a new block began, the location of future rewards, or how rewards were distributed within or across blocks.
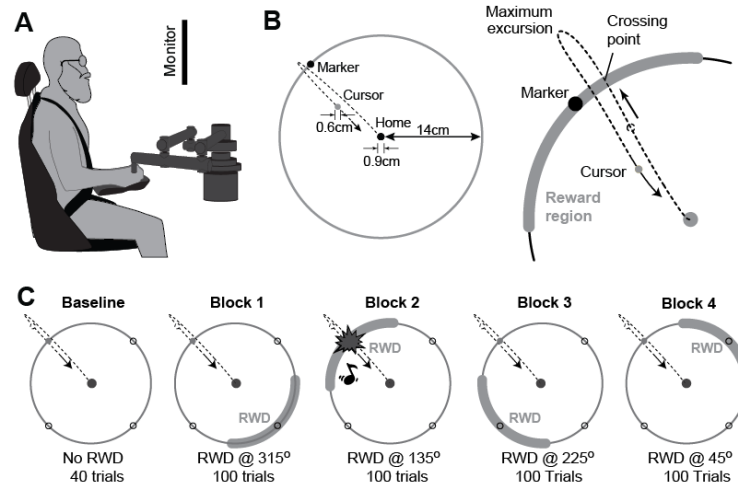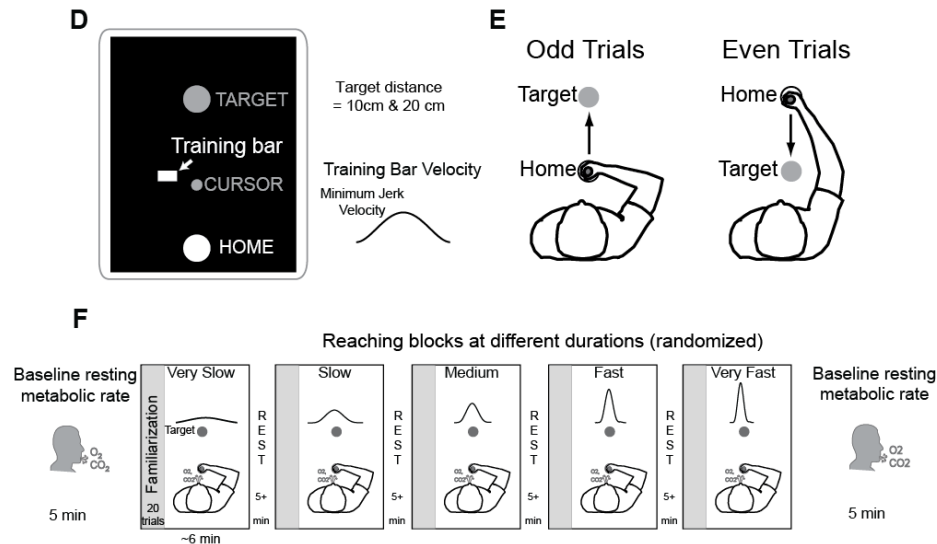
Figure 6.1 Designs for experiments 1 (A-C) and 2 (D-F). A) Set-up: Older aged adults controlled a cursor projected on a monitor by moving a robotic manipulandum with their right hand along the horizontal plane. B) Participants completed out-and-back reaches to alternating targets projected along a ring 14cm from the home circle. C) Protocol for experiment 1: The protocol consisted of a baseline period with no reward followed by four experimental blocks. Each experimental block had one quadrant paired with a reward (RWD). D) Virtual environment for experiment 2. Participants moved a cursor at constrained velocities between a home circle and a target. E) The direction of the reach alternated every trial. F) Protocol for experiment 2: Metabolic rate of the participant was measured first during seated rest, then while completing reaching movements at five different prescribed speeds; very slow (VS), slow (S), medium (M), fast (F), or very fast (VF). There was a short break between each block to allow the metabolic rate to return to rest. The order of blocks in the current figure are displayed in increasing order, however the actual block order was randomized for each participant.

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*Experiment 2: Effects of duration and distance on the metabolic cost of reaching*

Participants were seated in a position identical to experiment 1 (Figure 6.1A). Using the robotic handle, they made alternating out and back movements along the anterior-posterior axis (Figure 6.1D). For odd numbered trials, the movement was away from the body and on even numbered trials, the movement was back towards the body (Figure 6.1E). A trial began by placing the cursor over a home circle. After a 150ms delay, a circular target (diameter=1.6cm) appeared and the participant was instructed to move the cursor to the newly projected target. Unlike in experiment 1, participants executed their movements in this experiment according to two prescribed distances, each with five prescribed durations. The distances were 10cm and 20cm. The five movement durations used at each distance are referred to here on as very slow (VS), slow (S), medium (M), fast (F), and very fast (VF) (Figure 6.1F). The exact duration and number of trials depended on the reaching distance as well as age group (Table 1). The number of trials was selected to allow for ~6 minutes of reaching for each condition, with faster duration conditions requiring more trials. All twelve older adults reached at both distances over two days, with only a single distance tested each day.

| Table 1 Constrained movement duration and trial number by age and distance. | | | | | |
|---|---|---|---|---|---|
| Duration (ms) / Trial # | Very Slow | Slow | Medium | Fast | Very Fast |
| Young @10cm | 1000/180 | 775/200 | 500/230 | 350/260 | 125/300 |
| Older @10cm | 1100/180 | 800/210 | 600/230 | 500/245 | 250/260 |
| Young @20cm | 2050/140 | 1150/160 | 800/200 | 500/230 | 250/260 |
| Older @20cm | 2150/130 | 1250/170 | 850/210 | 550/230 | 250/250 |

Participants learned the desired duration for each condition based on two different feedback sources. The first was a training bar that would accompany the cursor along the left side of the movement path for the first four of every twenty trials. Upon

movement initiation, this training bar would follow a minimum jerk trajectory towards the target indicating the prescribed reaching velocity (Figure 6.1D). The second source of feedback was a change of target color once the cursor made contact with the target. If the cursor arrived within 50ms of the desired duration, the target would flash yellow and deliver a pleasing tone similar to the reward used in experiment 1. If the movement was too fast, the target would turn green and if the movement was too slow, it would turn gray.

Each visit in experiment 2 consisted of performing five blocks of reaching (Figure 6.1F). Within a visit, five durations were tested at a single distance. This means the metabolic profiles for each older adult was collected over two separate days. Three young adults participated in both visit, with the remaining 12 each participating in only one distance (n=7 at 10cm, n=8 at 20cm). A single reaching block consisted of 20 practice trials accompanied with the training bar, a short 1-minute break, then an additional ~6 minutes of reaching while wearing the nose clip and mouthpiece. Five-minute mandatory rest periods were included between blocks of reaching to allow an individual's metabolic rate to return to rest before the start of a new block. The constrained movement duration was consistent within each block and the block order was randomized for each participant.

*Data Analysis*

Position and velocity of the handle were recorded at 200 Hz. Reaction-time was calculated as the difference in time between when the audiovisual start stimulus was delivered and movement onset. Movement onset was identified using a threshold based

on radial acceleration of 0.0001 m/s$^2$ and radial velocity of 0.05 m/s. I measured the signed difference in degrees from the right horizontal, between the center of the quadrant and where the hand crossed the outer ring and refer to this angle as the crossing-point distance. The maximum Euclidean displacement of the cursor from the center determined the maximum excursion. Peak instantaneous outward velocity was identified between movement onset and the timepoint of maximum excursion.

Trials with reaction times greater than 700ms or with crossing-point distances outside of the 100 quadrant were removed from analysis. Across all older participants, this accounted for an exclusion of 4.32% of trials (332 trials for reaction time and 14 trials for crossing the outer ring in the incorrect quadrant).

Reaction time and velocity in experiment 2 was calculated in the same manner as experiment 1. The duration of each movement was calculated as the difference in time between the moment the individual reacted to the start cue (movement onset) and the end of movement was defined as the first moment after peak velocity where the anterior-posterior velocity reached zero. Total distance was measured as the difference in displacement between the position at movement onset and the position at the end of the movement. Inter-trial-interval (ITI) was measured between each trial as the time between the end of movement for the current trial and movement onset of the subsequent trial. This meant that ITI represented the combined time spent repositioning the cursor for the next trial and the reaction time of that same trial.

*Metabolic Cost*

In experiment 2, I quantified effort by measuring metabolic cost as a function of distance and duration. Metabolic cost was measured through expired gas analysis (ParvoMedics, TrueOne2400). Participants wore a nose clip and breathed in and out of a mouthpiece throughout all reaching bouts in experiment 2. This allowed me to measure how the rates of oxygen consumption and carbon dioxide production changed across conditions. To minimize the thermic effect of food on metabolic rate, all sessions were conducted in the morning with participants arriving having fasted overnight. The metabolic cart was calibrated at the start of each visit according to certified gas mixtures as well as a range of flow rates from a 3-litre calibration syringe. Baseline resting metabolic rate was measured while participants sat quietly in the chair holding the robotic handle. Baseline resting trials were taken at the start and end of the visit.

I calculated the gross metabolic rate of moving ($\dot{E}_{gross}$) and the gross metabolic rate of resting ($\dot{E}_{rest}$) in terms of watts (W) using the rate of oxygen consumption and carbon dioxide production according to the Brockway equation (Brockway 1987). I only included conditions where the respiratory exchange ratio was between 0.7 and 1.0, indicating aerobic respiration. I calculated net metabolic rate during each condition by measuring the gross metabolic rate ($\dot{E}_{gross}$) averaged over the last three minutes of reaching in each condition and subtracting the lower of the two metabolic rates measured during seated rest ($\dot{E}_{rest}$) at the beginning and end of the visit.

$$\dot{E}_{net} = \dot{E}_{gross} - \dot{E}_{rest} \qquad\qquad [\,6.1\,]$$

This net rate represented the combined cost of moving ($\dot{E}_{moving}$) and the cost of not moving when between each trial ($\dot{E}_{ITI}$):

$$\dot{E}_{net} = \dot{E}_{moving} + \dot{E}_{ITI}$$ [ 6.2 ]

If it is assumed that the net $\dot{E}_{ITI}$ is zero, then I am able to localize the net metabolic cost of moving the arm according to the equation:

$$\dot{E}_{moving} = \dot{E}_{net} \frac{ITI + d}{d}$$ [ 6.3 ]

Here ITI represents the average length of the inter-trial-interval (ms) and $d$ represents average movement duration (ms). I then fit the calculated net metabolic rate of moving according to the following function:

$$\dot{E}_{move} = a + b \frac{dist^c}{dur^d}$$ [ 6.4 ]

where cost increased as a function of distance (dist) and decreased as a function of duration (dur). Of the four free parameters, $a$ represents the asymptote, $c$ represents the contribution of distance and $d$ represents the contribution of duration towards the net metabolic cost of moving. The free parameter $b$ describes an overall effect of changing velocity on the metabolic cost of moving.

*Statistical analysis*

Experiment 1: The effect of reward for each individual was quantified by comparing the average peak velocity, reaction-time, maximum excursion, and crossing-point of each reaching movement towards a quadrant when it was rewarded minus when that same quadrant was not rewarded. Similarly the variance in reaction-time, time to circle, maximum excursion, and crossing-point were measured and compared

between rewarded and non-rewarded movements. The effect of reward was measured using a three-way repeated-measures analysis of variance (ANOVA) using age group (binary), block number (discrete), reward status (binary), a reward-by-age interaction, an-age-by block interaction, and an age by block by reward interaction as predictors. Rewarded movements were further compared to non-rewarded movements in the trials immediately before and after for both age groups using a paired t-test.

Experiment 2: The net metabolic cost of moving, $\dot{E}_{moving}$, was parameterized according to equation 6.4. The best fit model was determined according to minimization of the sum of squared error. To determine the effect of age on the net metabolic cost of moving, responses were fit independently for each age group as a function of distance and duration. I then compared best parameter fits for each age based on overlapping 95% confidence intervals.

I estimated the masses of the upper arm, lower arm and hand of each participant using previously published equations according to sex, body mass, and age (de Leva 1996; Chambers et al. 2010). The effect of age on the estimated masses of each segment was tested using a two-sample independent t-test.

All statistical thresholds were conducted at a significance level of $\alpha=0.05$. Uncorrected p-values reaching statistical power were corrected for multiple comparisons using the Holm-Bonferroni method. ANOVAs and paired t-tests were corrected for a total of 4 comparisons, established based on the number of measured behavioral responses (reaction-time, time to circle, crossing point, and maximum excursion). Descriptive statistics are reported as mean ± standard error.

## 6.4 Results

I sought to understand how increasing age affects the influence of reward and effort on reach vigor. I probed this question in a series of experiments involving groups of young (18-35 years) and older (66-87 years) adults.

*Effect of age on movement initiation towards reward*

The start of each trial was indicated simultaneously with an auditory presentation of a short tone and visual presentation of the outer red ring (radius=14cm). With increasing age, the 'sensory fitness' of audio and visual organs decline and the ability to react to stimuli of these modalities is reduced (Koga and Morant 1923). To measure the effects of age on movement initiation for both rewarded and non-rewarded movements, I calculated reaction time distributions for each condition (reward and no reward) as well the effect of age on the mean and variance of these distributions (Figure 6.2A). Independent of reward, I observed that older adults took longer to initiate their reaching movements. The average reaction time for a non-rewarded trial for older adults was 417±14ms, significantly longer than the reaction times of 302±40ms observed in young adults (Figure 6.2B, RM-ANOVA, main effect of age, $F(1,38,)$ $p<0.001$). Not only did older adults on average react slower than young adults, but they also exhibited higher reaction time variance (Figure 6.2C, main effect of age, $F(1,38)= 32.27$, $p<0.001$). These differences are collectively evident in the lower, wider, and later peaks for the probability density functions in older adults for the non-rewarded conditions (Figure 6.2A).

In expectation of reward, older adults responded by reacting earlier, in a similar manner to the young adults (Figure 6.2B inset, $\Delta_{young}$=-15±1ms, $\Delta_{old}$=-22±4ms; main effect of reward F(1, 38)=65.527, p<0.001, reward*age interaction, F(1,38)=1.964, p=0.169,). Older adults also decreased the variance in their reaction times and did so to a greater extent than the young adults (Figure 6.2C inset, $\Delta_{young}$=-0.9±0.3ms$^2$, $\Delta_{old}$=2.3±0.4ms$^2$; reward*age interaction, F(1,38)=8.118, p=0.007).

To further explore whether the magnitude of reward's effect on variance changed as a function of reaction time and age, I calculated reaction-time distributions in the form of a delta plot (Ridderinkhof et al. 2005). I divided the density function of each condition into 20% quantiles and calculated the difference in means at each quantile (rewarded minus non-rewarded) as a function of the average non-rewarded reaction time of that quantile (Figure 6.2D). The difference between reward and non-rewarded conditions became increasingly negative with higher quantiles. A similar slope describing these changes both within each age group as a function of increasing reaction time as well as between age groups, further suggests that the magnitude of the effect of reward on reaction time was consistent across quantiles and was independent of age. The similarities in slopes also suggest that the different reward-induced changes in reaction time variance between groups was likely due to the older adults having a generally more variable reaction time distribution.

Taken together, older adults initiated movements earlier and more consistently when executed in expectation of reward, similar to what has been observed in young adults. These findings suggest that the effect of reward on movement initiation is maintained with increasing age.
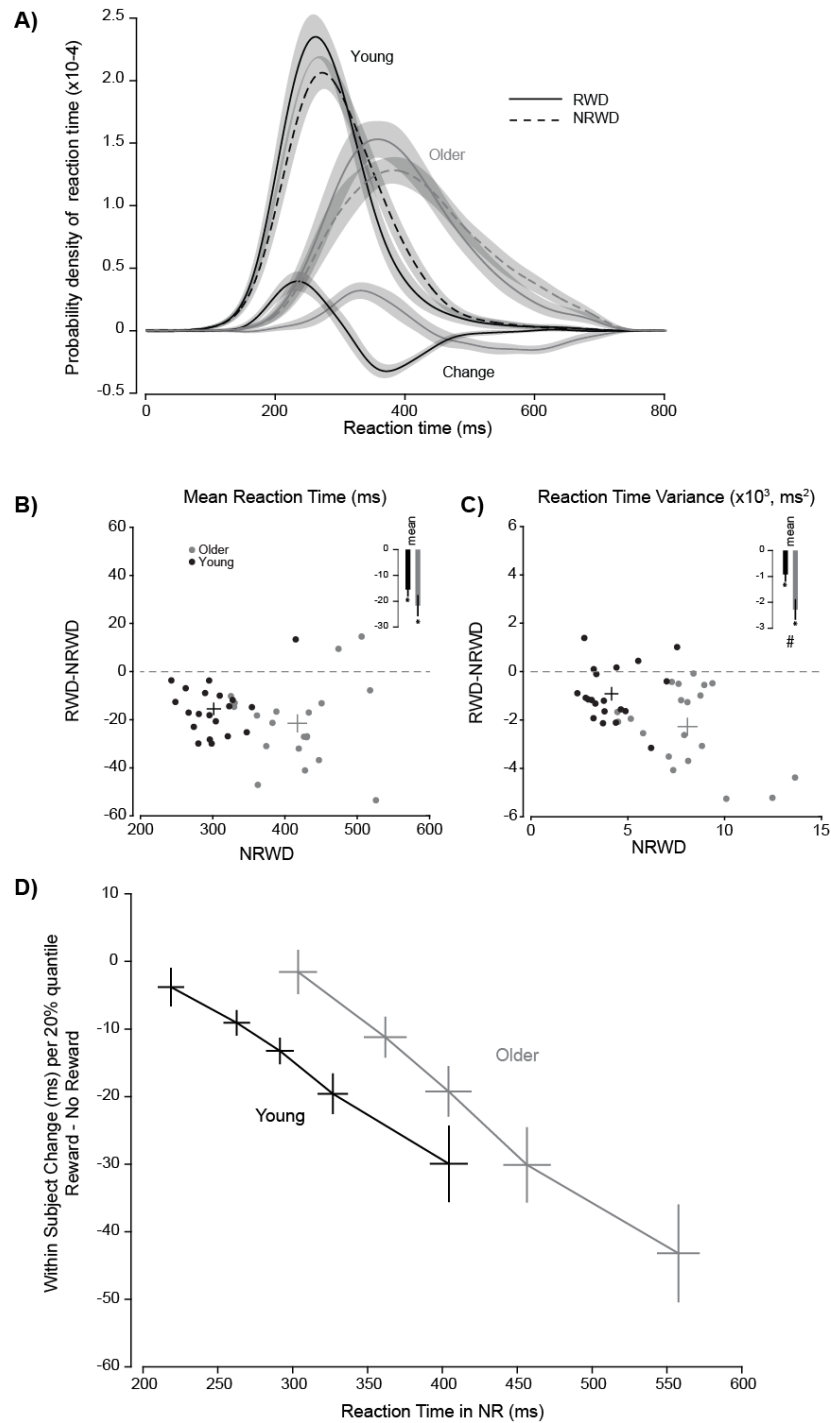
Figure 6.2 Effects of reward on movement initiation in young (black) and old (gray) adults. A) I used a non-parametric kernel density estimation method to calculate the probability distribution for each individual when making movements to rewarded (RWD, solid curves) and non-rewarded (NRWD, dashed curves) quadrants as well as a difference in these distributions at each bin (Older adults=gray, young=black, bin size=5ms). B) Scatter plot representing the relationship between rewarded (RWD, vertical axis) and non-rewarded (NRWD, horizontal axis) movements according to mean

reaction time. Dots represent individual participants (young=black, older=gray). The intersection at each cross represents the mean for each age group and the length of the bars represent ±SEM. The mean effect of reward for each age group is indicated with the inset bar graph, reported as mean ± SEM (* p<0.05, n.s. p>0.05, difference compared to zero; # p<0.05, difference between age groups). C) Same as B), but with reaction time variance being reported. D) Delta plot conveying the change in reaction time within each participant as a function of increasing 20% quantiles. The horizontal axis represents the mean NRWD reaction time at each quantile. The vertical axis represents the difference in reaction time (RWD-NRWD) for each age group at each quantile. Error bars represent ±SEM.

*Effect of age on movement execution towards rewarded and non-rewarded quadrants*

In experiment 1, both young and older adults were allowed to self select the velocity and extent of their movements (Figure 6.3). In the absence of reward, I found that older adults executed their movements in a manner that was similar to the younger adults. Specifically, I found no difference in time to circle (Figure 6.3C, main effect of age, $F(1,38)=3.467$ $p=0.070$) or maximum excursion (Figure 6.3D, $F(1,38)=0.182$, $p=0.672$).

If expectation of reward influenced the preparation of each movement for older adults, would the same effects be present during movement execution? I observed a main effect of reward on time to circle ($F(1,38)=10.038$, $p=0.009$) that was independent of age (reward*age interaction, $F(1,38)=4.634$, $p=0.465$). However, post-hoc comparisons between rewarded and non-rewarded movements revealed an effect of reward on time to circle in only the younger adult group (Figure 6.3C inset, $p_{young}=0.002$, $p_{older}=0.217$). The effect of reward on maximum excursion followed a similar trend with a main effect of reward ($F(1,38)=35.100$, $p<0.001$), but also an interaction between age and reward ($F(1,38)=12.18$, $p=0.005$). Again, post-hoc comparisons revealed greater maximum excursions due to reward in young adults, but not in older adults (Figure 6.3D

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inset, $p_{young}$<0.001, $p_{older}$=0.138). Taken together, older adults responded to reward by selecting a time to circle and maximum excursions that were both statistically indistinguishable from their non-rewarded movements. Reward had no effect for older adults on the observed variance of either time to circle or maximum excursion (p's>0.05).

The audiovisual reward used in the current experiment has previously been shown to influence the execution of reaching movements in young adults by 2-5%. Specifically young adults reached towards reward with a shorter time to circle and larger maximum excursion, both without altering crossing-point distance (Summerside et al. 2018). These findings collectively suggest that sensitivity to reward, in regards to its effects on movement execution, is diminished in older adults when compared to the effects of an identical reward with younger adults.
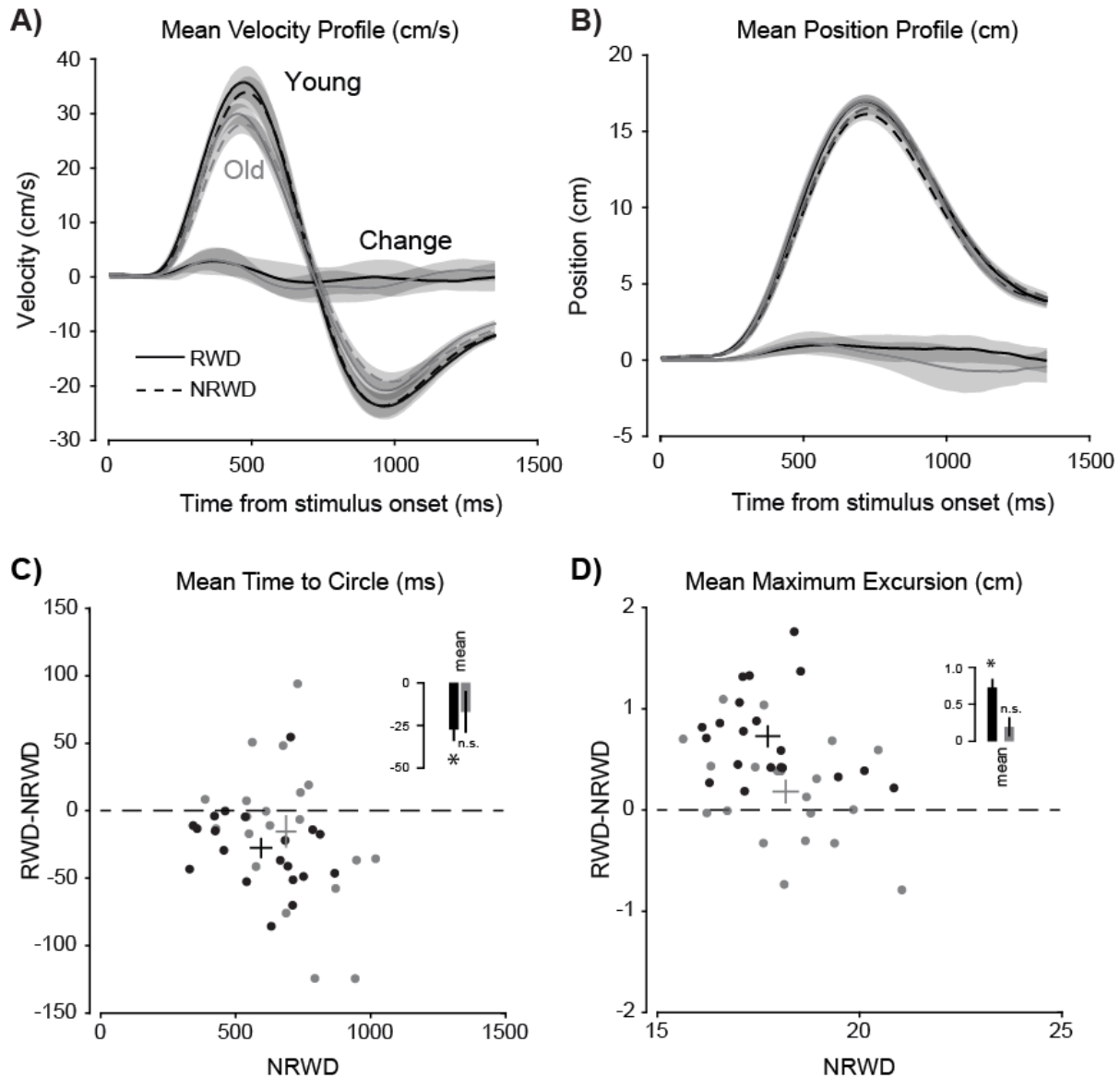
Figure 6.3 Effects of reward on movement execution in young (black) and older (gray) adults. A) Mean radial velocity of hand as a function of time. B) Mean radial position as a function of time. C) Scatter plot representing the relationship between rewarded (RWD, vertical axis) and non-rewarded (NRWD, horizontal axis) movements according to mean time to circle (ms). Dots represent individual participants. The intersection at each cross represents the mean for the age group and the length of the bars represent ±SEM. The mean effect of reward for each age group is indicated with the inset bar graph, reported as mean ± SEM (* p<0.05, n.s. =not significant, difference compared to zero). D) Same analysis as C), but with maximum excursion.

*Age and temporal proximity to reward*

I previously reported that in young adults, the effects of reward on vigor were confined to the rewarded movement itself, with no interactions with the trials immediately preceding (R-1) or following (R+1) reward (Summerside et al. 2018). Here, I examined whether older adult participants would behave similarly. Older adults had earlier reaction times towards rewarded quadrants, when compared to non-rewarded trials preceding (Figure 6.4A, $p_{R-1}<0.001$) and following ($p_{R+1}<0.001$) reward. Rewarded trials were also more consistent than surrounding non-rewarded trials in respect to reaction time variance (Figure 6.4B, $p_{R-1}<0.001$, $p_{R+1}=0.016$) and crossing-point variance (Figure 6.4F, $p_{R-1}=0.015$, $p_{R+1}=0.007$). There were no differences between rewarded and surrounding non-rewarded trials for time to circle (Figure 6.4C, $p_{R-1}=0.727$, $p_{R+1}=0.057$), maximum excursion (Figure 6.4D, $p_{R-1}=0.669$, $p_{R+1}=0.321$), or average crossing-point distance (Figure 6.4E, $p_{R-1}=0.311$, $p_{R+1}=0.901$).

To further probe the effect of age, I directly compared the relative changes in behavior between groups at the trial preceding reward and also at the trial following reward. At the trial preceding reward, there was no effect of age in response magnitude for reaction time (Figure 6.4A subset, $p=0.182$), reaction time variance (Figure 6.4B subset, $p=0.073$), time to circle (Figure 6.4C subset, $p_{uncorrected}=0.037$, $p_{corrected}=0.111$), crossing point (Figure 6.4E subset, $p=0.812$), or crossing point variance (Figure 6.4F subset, $p_{uncorrected}=0.035$, $p_{corrected}=0.105$). The difference in maximum excursion between reward and the trial preceding reward was greater in younger adults (Figure 6.4D subset, $p_{R-1}=0.008$). When comparing age groups at the trial following reward, I found no effect of age in response magnitudes for reaction time (Figure 6.4A subset,

p=0.770), reaction time variance (Figure 6.4B subset, p=0.724), time to circle (Figure 6.4C subset, p=0.572), crossing point (Figure 6.4E subset, p=0.597), or crossing point variance (Figure 6.4F subset, p=0.257). The change in maximum excursion following reward was greater in younger adults when compared to older (Figure 6.4D subset, p=0.020).

Figure 6.4 Effect of temporal proximity to reward in young (black) and older (gray) adults. Change in A) mean reaction time (ms), B) variance in reaction time (ms$^2$), C) mean time to circle (ms), D) mean maximum excursion (cm), E) mean crossing point distance (deg), and F) variance in crossing point distance (deg$^2$) in trials immediately preceding (R-1) and following (R+1) reward. Values reported as relative changes from reward (* $p<0.05$, ** $p<0.01$, *** $p<0.001$, n.s.=not significant). Subset graphs represent relative differences (older adults minus young adults) in response magnitude between age groups at each trial (OA=older adults, YA=young adults, # $p<0.05$, *c* significant difference lost as a result of correcting for multiple comparisons). Error bars represent ±SEM and have been slightly offset horizontally to improve contrast.

*Age and the effect of time on vigor*

The experiment consisted of participants completing over 400 reaching movements. To explore whether the length of the experiment affected reaching movements, I performed a repeated measures ANOVA where all behavioral measures were predicted according to the combined effects of reward, age, and block number.

As the experiment progressed, the mean reaction time decreased (Figure 6.5A, main effect of block, (F(3,144)=6.581, p<0.001) and this change was independent of reward or age (block-by-age, block-by-reward, block-by-reward-by-age interactions, p's>0.05). Reaction time variance appeared to decrease as well, however this effect was lost when correcting for multiple comparisons (Figure 6.5B, F(3,144)=3.329, $p_{uncorrected}$=0.022, $p_{corrected}$=0.066). There was no effect of reaction-time variance on any interactions with block (block-by-age, block-by-reward, block-by-reward-by-age interactions, p's>0.05). These results suggest that the duration of the experiment influenced movement preparation, but that this change was independent of either reward status or age.

The progression of the experiment also influenced aspects of how individuals executed their reaching movements. Time to circle decreased throughout the experiment (Figure 6.5C, main effect of block, F(3,144)=15.300, p<0.001) and was also independent of age (block-by-age interaction, F(3,144)=0.307, p=0.821) or reward (block-by-reward, F(3,144)=0.481, p=0.696; block-by-reward-by-age interaction, F(3,144)=0.343, p=0.794). Maximum excursion, mean crossing point, and crossing-point variance were all consistent throughout the course of the experiment (Figure 6.5D-

F, main effect of block, block-by-age, block-by-reward, block-by-reward-by-age interactions, p's>0.05).

Overall, the length of the experiment influenced certain aspects of movement execution, however, this change was independent of either reward or age. Importantly, the observation that older adults increased the velocity of their reaching movements throughout the course of the experiment indicates that the reluctance to alter the execution of their movements towards reward was not due to a limit in the capacity of the older adults to increase vigor, but rather due to an age-specific effect in the value assigned to the reward stimulus.
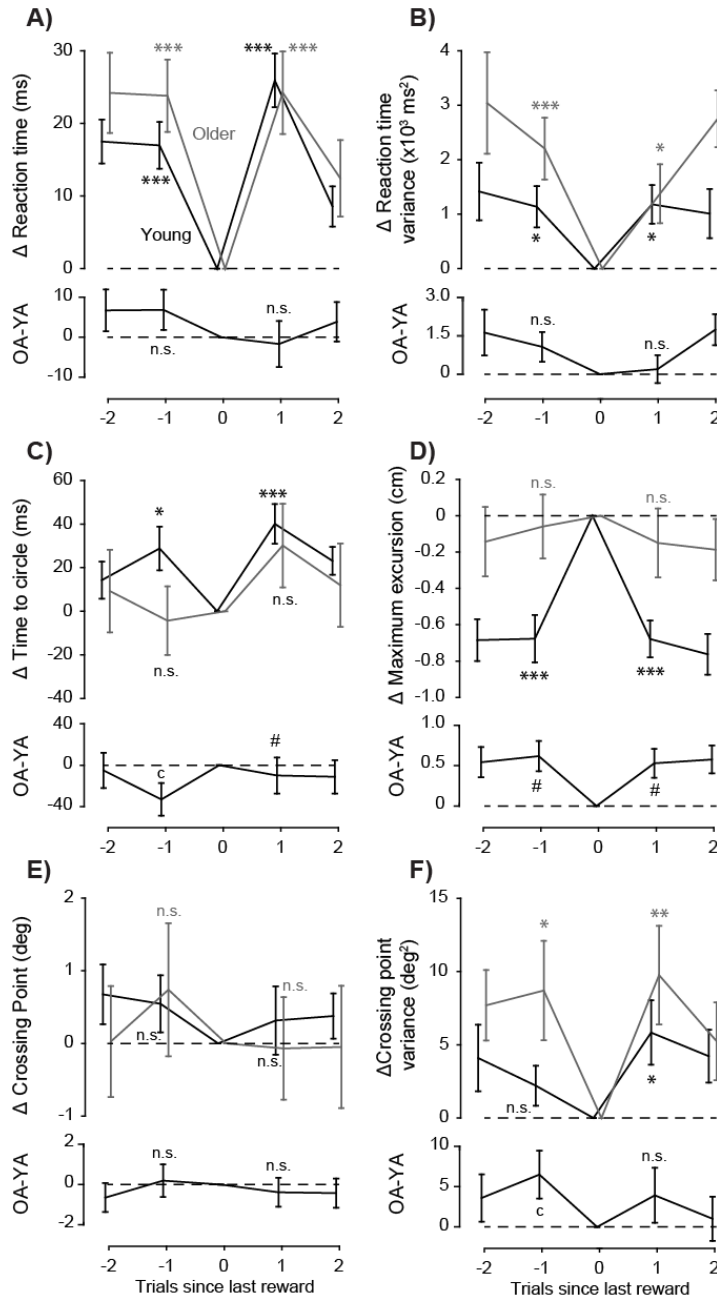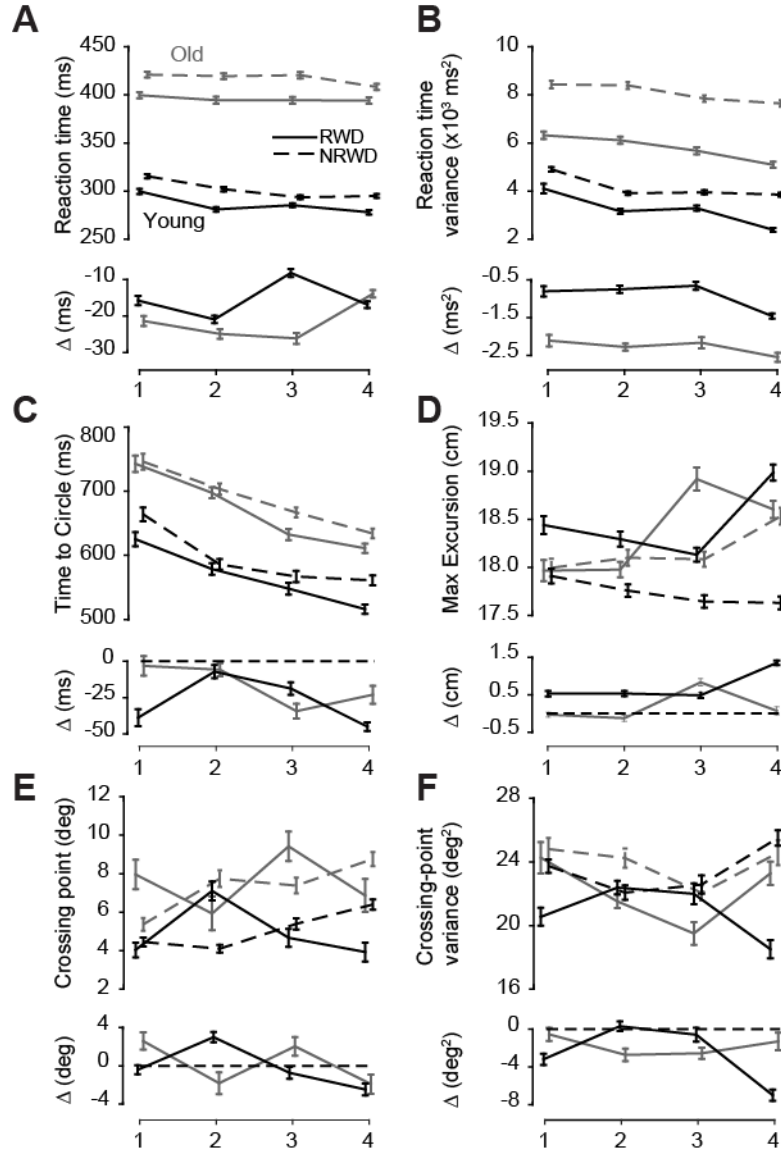
Figure 6.5 Effect of temporal proximity to reward in young (black) and older (gray) adults. Change in A) mean reaction time (ms), B) variance in reaction time ($ms^2$), C) mean time to circle (ms), D) mean maximum excursion (cm), E) mean crossing point distance (deg), and F) variance in crossing point distance ($deg^2$) in trials immediately preceding (R-1) and following (R+1) reward. Values reported as relative changes from reward (* $p<0.05$, ** $p<0.01$, *** $p<0.001$, n.s.=not significant). Subset graphs represent relative differences (older adults minus young adults) in response magnitude between age groups at each trial (OA=older adults, YA=young adults, # $p<0.05$, *c* significant difference lost as a result of correcting for multiple comparisons). Error bars represent ±SEM and have been slightly offset horizontally to improve contrast.

*Effect of age on the metabolic cost of reaching*

Older adults did not adjust the velocity or extent of their reaching movements in response to added reward. This could be explained by a decreased sensitivity to the reward itself or due to an increased cost of effort when compared to younger adults. In the second experiment, I measured how the cost of reaching in older adults changed independently with increasing movement duration and distance and whether this response was dependent on age. I quantified the cost of effort objectively by measuring the metabolic rate of each reaching condition obtained via indirect calorimetry. I measured the metabolic rate of moving in older adults as they made alternating forward and return reaching movements at distances of 10 and 20cm and over durations ranging from 125 to 2250ms and compared their performance to previously collected young adult data (Table 6.2, Figure 6.6).

**Table 6.2 Durations, inter-trial-intervals (ITI) and metabolic rates across conditions**

***Young Adults (4F, 3M, 66±5kg) at 10cm***

| Intended Durations= | 1000ms | 775ms | 500ms | 300ms | 125ms |
|---|---|---|---|---|---|
| Actual Duration (ms): | 1154±9 | 952±16 | 637±14 | 434±11 | 369±9 |
| ITI (ms): | 909±43 | 761±26 | 800±22 | 775±10 | 789±8 |
| Gross Rate (J/s): | 95±6 | 97±6 | 98±5 | 113±6 | 128±4 |
| Net Rate (J/s): | 16±2 | 18±3 | 19±2 | 33±3 | 48±4 |
| Moving Rate (J/s): | 27±3 | 32±5 | 42±4 | 93±10 | 152±14 |

Resting Rate (J/s): 79±5

***Young Adults (4F, 4m, 66±3kg) at 20cm***

| Intended Durations= | 2050ms | 1150ms | 800ms | 500ms | 250ms |
|---|---|---|---|---|---|
| Actual Duration (ms): | 2141±15 | 1339±13 | 960±11 | 625±16 | 478±17 |
| ITI (ms): | 1137±44 | 842±20 | 763±12 | 794±6 | 806±9 |
| Gross Rate (J/s): | 94±5 | 97±4 | 100±4 | 114±4 | 140±5 |
| Net Rate (J/s): | 13±4 | 16±3 | 19±4 | 33±5 | 59±7 |
| Moving Rate (J/s): | 20±5 | 27±5 | 34±8 | 74±11 | 158±15 |

Resting Rate (J/s): 81±5

***Older adults (6F, 6M, 71±6kg) at 10cm***

| Intended Durations= | 1100ms | 800ms | 600ms | 500ms | 250ms |
|---|---|---|---|---|---|
| Actual Duration (ms): | 1129±27 | 924±18 | 728±17 | 657±15 | 522±17 |
| ITI (ms): | 1235±119 | 1094±63 | 1081±51 | 1142±73 | 1289±66 |
| Gross Rate (J/s): | 79±5 | 82±5 | 86±5 | 90±5 | 96±6 |
| Net Rate (J/s): | 8±2 | 11±2 | 15±3 | 19±4 | 25±4 |
| Moving Rate (J/s): | 16±5 | 26±7 | 38±11 | 55±16 | 88±26 |

Resting Rate (J/s): 71±5

***Older adults (6F, 6M, 71±6kg) at 20cm***

| Intended Durations= | 2150ms | 1250ms | 850ms | 550ms | 250ms |
|---|---|---|---|---|---|
| Actual Duration (ms): | 2081±49 | 1347±26 | 990±19 | 707±24 | 635±15 |
| ITI (ms): | 1197±54 | 1056±60 | 1031±54 | 1031±48 | 1153±47 |
| Gross Rate (J/s): | 83±5 | 85±5 | 89±5 | 99±6 | 109±7 |
| Net Rate (J/s): | 15±2 | 18±3 | 22±3 | 32±5 | 39±5 |
| Moving Rate (J/s): | 24±2 | 33±5 | 44±6 | 83±12 | 109±14 |

Resting Rate (J/s): 68±5

In line with previous findings (Shadmehr et al. 2016), the variance in the net metabolic cost of reaching was strongly explained as a function of distance and duration ($R^2$=0.82). As the duration towards a set target distance increased, the net metabolic rate of moving decreased ($c$=0.68 [0.37 1.00], p<0.001). Similarly, for movements of a set duration, increasing distance resulted in an increase in the net metabolic cost of moving ($d$=1.61 [0.99 2.24], p<0.001). There was no significant offset ($a$=1.52 [-20.79 23.83], p=0.89). The free parameter $b$ was 129.35 [72.82 185.88] (p<0.001).

To test whether the metabolic response to these constrained movements was age-dependent, I fit the net metabolic cost of moving independently for each age group (Figure 6.6AB). Models for each young and older adults explained a large amount of variance in metabolic cost (young $R^2$=0.88, older $R^2$=0.78). Both age groups equally responded to changing distance ($c$, young=0.69 [0.27 1.12] p=0.002, older=0.91 [0.27 1.55] p=0.004) and duration ($d$, young=1.98 [1.01 2.96] p<0.001, older=2.03 [0.57 3.48] p=0.007). Furthermore, there was no difference in either $a$ (young=10.79 [-12.83 34.41], older= 7.39 [-22.09 36.88]) or $b$ (young=87.10 [27.32 146.88], older=160.10 [53.29 266.91]).

If I use the same model structure to explore and age dependent difference in the gross metabolic cost of moving ($\dot{E}_{moving}+\dot{E}_{rest}$), I obtain a similar outcome (Figure 6.6DE). Models resulting from each age group adequately captured the variance in the gross metabolic cost of moving (young $R^2$=0.97, older $R^2$=0.93). Again, metabolic cost in both groups increased in response to increasing distance ($c$, young=0.80 [0.41 1.19] p<0.001, older=0.86 [0.22 1.51] p=0.009) and decreased in response to increasing duration ($d$, young=2.22 [1.32 3.11] p<0.001, older=2.06 [0.54 3.58] p=0.008). However,

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there was now a significant asymptote (representative of $\dot{E}_{rest}$) that was similar for both groups (*a*, young=94.28 [76.15 112.41] p<0.001, older=77.48 [47.59 107.38] p<0.001). There was still a significant effect of parameter *b* (younger=87.25 [33.72 140.78] p=0.002, older=143.17 [41.73 244.60] p=0.006). When directly comparing the resting metabolic rate of each age group, I found they were at levels that were statistically indistinguishable, but which appeared to approach significance (young=78.83±3.50, older=68.83±4.56, independent t-test, p=0.068).

The common findings of these models suggest that the metabolic cost of reaching (1) decreased as a function of movement duration, (2) increased as a function of distance, and (3) appeared to be conserved as a result of healthy aging.
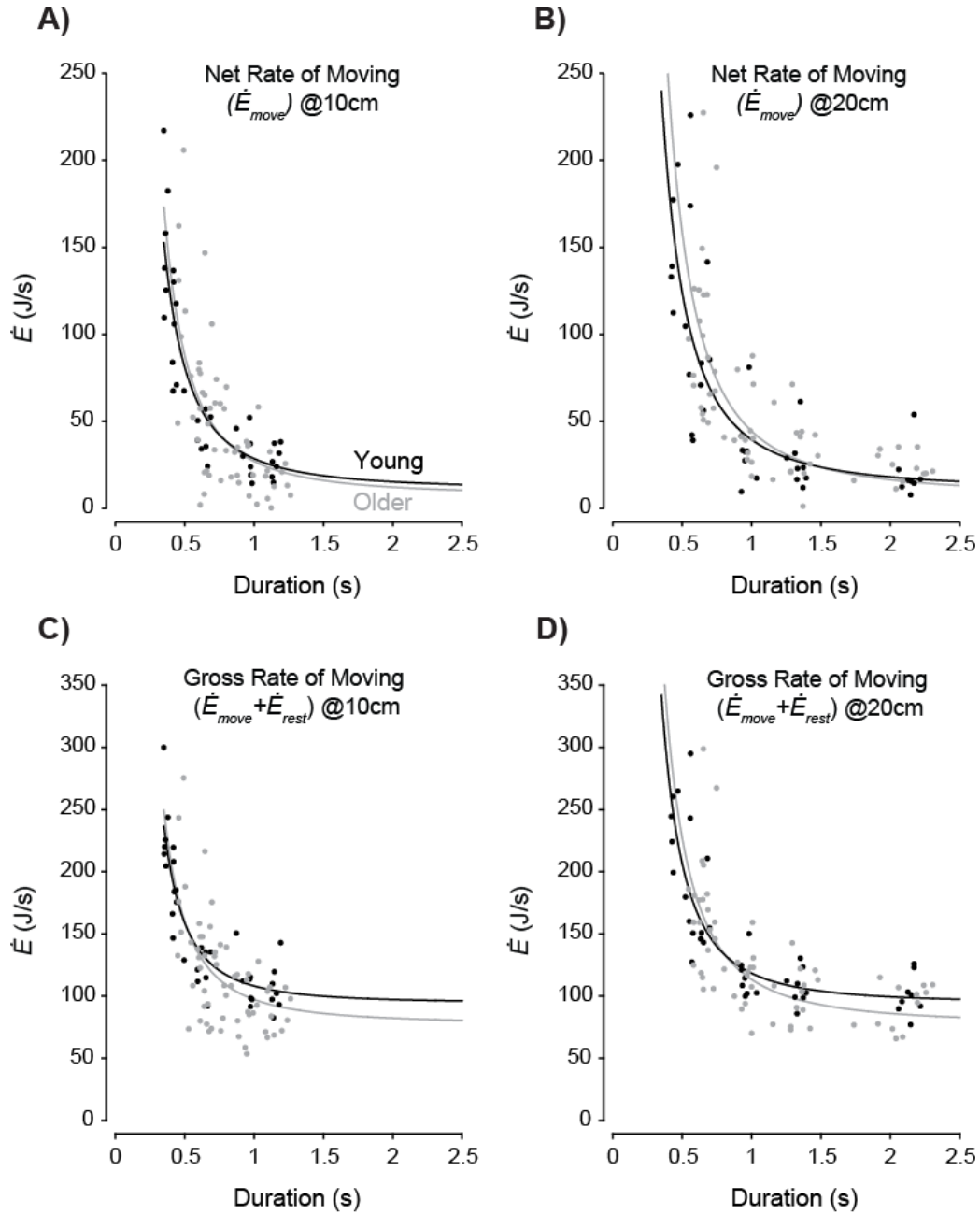
Figure 6.6 Effect of duration, distance, and age on the metabolic rate of moving. Dots represent individual means (black=young, gray=older). Panels A and B represent changes in net costs and panels C and D represent changes in gross costs. Curves represent model results for each age.

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*Masses of arm segments are equal between age groups*

The mass of the arm influences the metabolic cost of reaching across distance and duration (Shadmehr et al. 2016). To explore whether differences in segment mass could account for the lower metabolic cost observed at the short distance/slow duration condition, I estimated the segment masses of each participant's right arm as a function of weight, age, and sex. Based on these estimates, there appeared to be no difference in segment masses between younger and older adults for the upper arm ($m_{young}$=1.76±0.28kg, $m_{old}$=1.74±0.42, p=0.88), lower arm ($m_{young}$=1.00±0.19kg, $m_{old}$=1.11±0.36, p=0.32) or hand ($m_{young}$=0.39±0.07kg, $m_{old}$=0.41±0.12, p=0.53). These results suggest that the influence of mass on the measurement of metabolic cost was similar between the young and older age groups.

*Reduced sensitivity to reward in older adults is not explained by greater effort*

The results of experiment 2 allowed for further interpretation of the mechanism underlying the reduced effect of reward in older adults observed in experiment 1. Despite being aware of the presence of reward, as evident in the reward-induced changes in movement initiation, reward had a significantly weaker effect on how older adults selected the vigor of their movements. The reduced reward sensitivity could potentially be explained by a greater objective effort cost of movement execution. Across all trials in experiment 1, older adults averaged a maximum excursion of 18.2±0.3cm with a time to circle of 672±35ms. Young adults averaged a maximum excursion of 17.9±0.3cm with a time to circle of 588±37ms. If I use these durations and the model fits from experiment 2 to estimate the net metabolic cost of reaching, I see

that the young and older model predictions strongly overlapped (Figure 6.6B). I used the parameter values obtained from each age group to predict the net metabolic cost of reaching in experiment 1. Based on these estimates, I found no distinguishable difference in the mean metabolic cost of moving between age groups (young=112±15J/s, older=99±13J/s, p=0.938). Thus the older adults' weaker modulation of movement velocity and extent in response to reward do not appear to be a result due to differences in objective effort.

## 6.5 Discussion

I observed that older adults, like young, decreased the mean and variance of their reaction times in expectation of reward. However, when executing movements towards increased reward, only younger adults adjusted the velocity and extent of their reaching movements. This reluctance for older adults to adjust movement execution could not be explained by an increase in the cost of objective effort. I measured the metabolic cost of reaching as a function of changing duration and distance and found that these responses were not elevated as a result of healthy aging. In the following section, I discuss evidence supporting the idea that the reluctance for older adults to modulate vigor in response to reward can be better explained by a decreased sensitivity to the reward itself rather than an increase in effort associated with increasing vigor.

*Reward alters movement preparation in both groups, but not execution*
With increasing age, the 'sensory fitness' of audio and visual organs decline and the ability to react to stimuli of these modalities is reduced (Koga and Morant 1923). One

explanation for why older adults did not adjust the execution of their movements in response to reward could be that the audiovisual qualities of the reward were not processed in the same manner as in younger adults, leading to a decrease in the value of these stimuli. Alternatively, older adults may have adequately perceived the rewarding stimulus, and rather the observed differences in response to reward were due to different added value assigned to the rewarding stimuli (Dreher et al. 2008). I found that older participants decreased reaction time in expectation of reward, but did not increase velocity or extent when executing reaching movements towards those quadrants. These results indicate that older individuals adequately perceived the added stimuli in the rewarded quadrants, supporting the hypothesis that in older adults, the sensitivity to the rewarding qualities of the stimuli were relatively under valued when compared to younger adults. Furthermore, the manifestations of this age dependent difference in values become apparent more so in the execution rather than preparation aspect of the movement.

*Older and young adults executed movements similarly towards non-rewarded quadrants*

I found no differences between the two age groups when selecting velocity or extent of their movements in the absence of reward. These findings go against previously reported observations showing an age dependent decrease in execution across a range of representative movements (Waters et al. 1988; Ketcham et al. 2002; Kozak et al. 2003; Laufer 2005; Irving et al. 2006; Huang and Ahmed 2013; Dowiasch et al. 2015). When making pointing movements, individuals adjust the velocity of their movements according to the size and amplitude of the endpoint (Fitts 1954). Ketcham

et al. (2002) reported that when reaching towards targets of decreasing size, older adults were slower and less accurate than young and were less willing to adjust the velocity of their movements in response to changing task difficulty. Kozak et al. (2003) measured preferred reaching velocity of older and young adults as they reached out to touched a button while standing on an elevated platform. In this environment, where the cost of stability was high, older adults preferred slower shorter reaches when compared to younger and were less willing to increase their reaching velocity when instructed. The current design minimized the cost of both accuracy and stability. First, participants made all movements while seated. This eliminated the consequences of increasing momentum as a result of more vigorous reaching. Second, the quadrants used were of a large size that allowed for a minimal influence of accuracy costs. As long as the movement was directed towards the correct quadrant, no amount of naturally occurring signal dependent or independent noise would cause a trial to fail. These two combined factors allowed me to mitigate the cost of accuracy or stability and focus instead on how effort and reward interact to establish vigor in older adults.

*Metabolic cost of reaching is conserved across age*

The metabolic cost of reaching has previously been shown to change as a function of distance and duration in younger adults (Shadmehr et al. 2016). However, to our knowledge, the results presented in the current study are the first to explore whether this change is age dependent. I confirm that changes in metabolic cost can be captured across a range of representative distances and duration, but furthermore, that this relationship is conserved between older and younger adults.

Across the tested conditions, I was able to elicit increases in gross metabolic rate ($\dot{E}_{gross}$) ranging between 18% and 75% of $\dot{E}_{rest}$ in young adults at 20cm and between 19% and 56% above rest in older adults at 20cm. I measured the metabolic rate of reaching across multiple conditions for each individual with the intention of minimizing the possibility of sensor error (~5% (Crouter et al. 2006)) in hiding potential age dependent differences. While I cannot for certain, eliminate the possibility that sensor error is masking age effects, I can confidently say that the effect of age on reaching is not affected to the same magnitude as other activities such as walking, where one study reported metabolic cost increasing by as much as 15% as a result of old age (Ortega and Farley 2015). Additionally, the fact that the measured mean metabolic cost was in most cases lower than the mean for younger adults, makes the possibility of an age dependent increase in metabolic rate even more unlikely.

My results do not exclude the possibility that there is an age dependent subjective inflation in the cost of effort, a possible explanation as to why older adults were not willing to adjust their movement velocity or extent. The dopaminergic midbrain has long been a target for the coding of reward value (Schultz et al. 1997; Tobler et al. 2005), with this region having been shown to decline in activity as a function of aging (Dreher et al. 2008; Chowdhury et al. 2013). However, recent evidence has also highlighted the role of this region in the representation of effort costs (Salamone et al. 1991b, 1994b; Phillips et al. 2007; Wardle et al. 2011; Treadway et al. 2012). Wardle et al. (2011) were able to identify a positive association between an individual's level of activity in their dopaminergic regions with their willingness to exert effort for a given reward. Similarly, individuals with decreased dopaminergic tone, such as individuals

with Parkinson's Disease, show a heightened sensitivity to effort, possibly explaining one of their cardinal symptoms, bradykinesia (Mazzoni et al. 2007; Schmidt et al. 2008b; Chong et al. 2015).

An increased sensitivity to effort may explain why older adults were less willing to increase their vigor in response to added reward, however, both age groups exhibited a similar level of vigor in movements towards unrewarded quadrants. This discrepancy leads me to believe that the reluctance of older adults to modulate their vigor in response to added reward was driven more by the sensitivity to the reward itself than by a subjective inflation in the cost of increasing effort.


*Interpreting net versus gross metabolic costs*

In the current study, I reported that the net metabolic cost of moving was not elevated in older adults when reaching across a range of distances and durations. My conclusions were drawn using net rate of moving rather than gross rate for two reasons. First, many participants made two visits to the lab, each on different days. Using net rather than gross rate allowed me to focus on differences caused by the effects of distance and durations, independent of potential day-to-day fluctuations in resting rate within participants (~4% in our older adults). Second, the resting metabolic rate of older adults has previously been reported to be lower than in younger adults (Fukagawa et al. 1990; Frisard et al. 2007). Though the average resting metabolic rate between age groups was indistinguishable in my current cohort, using net rather than gross metabolic rate allowed me to isolate changes in metabolic rate resulting specifically from the movement itself. It should be noted that whether using net or gross rate, the main

conclusions still hold, increasing speed increases the metabolic rate of moving and importantly, this cost does not appear to be elevated in older adults.

*Temporal discounting of reward*

Another interpretation of my results is that young and older adults similarly represented both the cost of effort and the value of the reward and that the observed differences in movement execution may be accounted for due to a difference in the cost of time (Shadmehr et al. 2010).  Temporal discounting is a concept where reward decreases in value the longer an animal must wait for it (Myerson and Green 1995). This decay has been modeled according to a hyperbolic discounting function (Haith et al. 2012):

$$V_{delay}(d) = \frac{\alpha}{1 + kd} \qquad [5]$$

Here, the temporally discounted value of reward ($V_{delay}$) is a function of delay ($d$), instantaneous value ($\alpha$), and a weighting variable representing impulsivity ($k$). Small values for $k$ suggest that an individual values a reward consistently across time. Other individuals who are more compulsive would have larger values of k, meaning they would be more likely to forgo a larger later reward for a smaller immediate reward. Furthermore, this function of temporal discounting predicts greater changes in value as a result of greater instantaneous value ($\alpha$). If I consider movement time to represent the delay before acquiring reward, then moving faster may require more effort, but it also minimizes the potential loss of reward due to the cost of time. Impulsivity is higher in younger ages and gradually declines until leveling out as we reach middle-aged adulthood (Green et al. 1996, 1999). Even if the cost of effort and instantaneous sensitivity to reward were equal across the tested ages, younger adults in the current

study may have chosen to increase their velocity to minimize the reward lost to temporal discounting, a change in value not perceived in the older adult group.

*Limitations*

The use of an audiovisual stimulus as the reward likely had a different effect on the older and younger group due to a decline in the ability to hear and see that accompany healthy aging. Even with an auditory and visual system expected of young adults, the benefits of the reward where relatively small, resulting in only a miniscule response in vigor of 2-5%. Two improvements to the current protocol should be considered for future studies. First, the reward should take a medium that is better controlled across age, for example a food or monetary reward. Second, the current reward was binary. Because I only used a binary reward design, I was unable to comment on whether an effect of reward was present, but just too small to detect, or alternatively, the reward truly had no effect in determining how to execute the movement. By introducing a multitude of reward magnitudes, I would better be able to elucidate whether the current absence of response in older adults was due primarily to reasons pertaining to changing effort or reward.

A few studies suggest that animals change behavior not just as a result of a change in reward quality, but also a change in reward rate (Niv et al. 2007; Haith et al. 2012). This means that the reward landscape can be additionally manipulated by changing the frequency of reward, either by changing the relative number of rewards, or the amount of time elapsed between trials. I did not control for inter-trial-interval in either experiment nor manipulate the number of rewards across blocks. Faster completion of

trials would result in a greater reward rate, which could explain why vigor in both age groups increased as experiment 1 progressed. Controlling inter-trial-interval has previously been shown to affect the vigor of saccades in young adults (Haith et al. 2012). A similar constraint implemented with older adults could further explain how they consider changing reward when establishing movement vigor.

I measured how the metabolic cost of reaching responded to changing distances and durations. Another important cost that I ignored was to change the mass at the end of the arm. All reaches occurred without any added mass from the robot. The only possible source of differences in mass could be due to different sizes in the arm segments between age groups. I did not directly measure these masses, but estimated them based on an individual's age sex and weight. My estimates indicated that there was no differences in mass between the two age groups. By adding additional mass to the robot, I can increase the amount of inertia required to overcome when moving the handle. This additional dimension would allow me to explore a larger cost landscape than what is possible by just changing the current kinematic constraints, further enabling me to probe how older adults value changing effort costs when establishing vigor.

Lastly, it is important to consider that my comparisons between older and young adults have been on an absolute level. As we get older, our capacity for aerobic exercise ($VO_{2max}$) declines (Dehn and Bruce 1972; Fleg and Lakatta 1988). Sparrow et al. (2005) found that young and older adults had similar reductions in absolute levels of metabolic rate when learning coordinated arm movements, but that the older adults maintained an increased heart rate. Therefore, I must consider the possibility that older adults did not respond to reward in the same manner as young due to a greater relative

change in regards to percent of their $VO_{2max}$. This explanation however, seems somewhat unsatisfactory, especially when considering that the two groups similarly executed movements towards non-rewarded quadrants.

**Conclusion**

In the current set of experiments I sought to understand how the interactions of changing reward and effort compared across different ages when making basic reaching movements. I found that the metabolic cost of reaching as a function of duration and distance was indistinguishable between age groups. When introduced with added reward, both younger and older adults responded by decreasing reaction time. When executing the movement towards reward, only younger adults increased their velocity and extent, with all responses ranging between 2 and 5 percent. I conclude that when moving in a dynamic reward landscape, older adults were aware of the changes in reward, but were less willing to increase the cost of effort in those movements to obtain the rewards sooner.

# CHAPTER 7

# THESIS CONCLUSIONS

1. In my first study, I explored how individuals valued effort when deciding between different risky reaching movements. When representing effort as the metabolic cost of the movement:

    a.  Individuals subjectively valued the increasing cost of effort non-linearly.

    b.  The subjective value of effort was idiosyncratic. Sensitivity to effort increased in half of the participants and decreased in the remaining half.

    c.  When considering the range of subjective distortions across participants, the behavior of the group was best described by an objectively valued effort cost.

    d.  Traditional optimal control models represent effort as a quadratically increasing cost. This quadratic representation of effort, when quantified as a metabolic cost, failed to explain the group's decision-making strategies.

    e.  The subjective valuation of effort is not distorted to the extent previously estimated when represented as metabolic cost.

2. In my second study, I developed a decision-making paradigm to measure how effort and time costs interacted when explaining gait selection. By observing the distances when individuals changed their gait preference, I found that:

    a.  Neither minimizing total movement time nor total metabolic energy adequately captured how the group made decisions between walking and running.

    b.  Gait decisions were best explained by minimizing a weighted combination of metabolic and temporal costs.

c. Individuals with a high weighting on time adjusted running speeds dependent on the temporal costs associated with each gait and individuals who heavily weighted effort selected gait speeds that were consistent across a range of temporal costs.

d. Adjustments in preferred velocity were only observed in running gaits where decreasing total time resulted in a relatively smaller increase in effort than in walking.

e. The subjective value of effort has implications for how individuals select movement speed.

3. In my third study, I measured how young adults altered the vigor of unconstrained reaching movements in response to a changing reward landscape. I measured an extensive collection of behavioral responses both in regards to movement preparation and movement initiation.

a. In expectation of increased reward, younger adults reacted faster and reached with a higher velocity and greater magnitude than similar movements made in the absence of reward.

b. Reward also lead to movements that were more consistent, an observation counter to what is predicted by the traditional speed-accuracy trade-off.

c. The effects of reward appeared to be localized to the rewarded movement itself, with no influence on subsequent movements or even return aspects of the same movement following reward delivery.

d. Even when reward quality is independent of the movement behaviors, individuals spent greater effort to acquire that reward sooner.

4. In my last study, I sought to understand how the representation of cost and benefits changed as a result of healthy aging when selecting movement vigor in a dynamic reward landscape.

    a. Increased reward led older adults to decrease reaction time similarly to young adults.

    b. Variability in reaction time also decreased in older adults in expectation of reward.

    c. When executing reaching movements towards reward, older adults had a diminished response when compared to young in regards to movement velocity and extent.

    d. Young and older adults had similar metabolic costs when reaching across a range of durations and distances.

    e. The diminished sensitivity to reward in older adults does not appear to be a result of increased objective effort costs, but instead more likely due to a diminished value of the reward itself.

Collectively, the presented research has introduced a swath of examples where changing the effort, time, and/or reward associated with a movement alters both the preference for that movement and the vigor of performing that movement. These results provide much needed human experimental data to support the relatively novel idea in motor control that movement is not simply the product of minimizing a single objective cost, but rather is the product of a complex interaction of internal constraints of the animal and the ever changing reward landscape of the animal's environment.

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