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On the generalization of decision-making preferences in movement under risk

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ON THE GENERALIZATION OF DECISION-MAKING PREFERENCES
IN MOVEMENT UNDER RISK

by

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ON THE GENERALIZATION OF DECISION-MAKING PREFERENCES IN MOVEMENT UNDER RISK

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

Abstract

Nearly every aspect of our behavior is framed by risk, and people can respond to risk very differently. Some individuals readily confront highly variable situations in order to obtain large rewards (risk-seeking behavior), while others prefer more certain situations even if it means obtaining smaller rewards (risk-averse behavior). At present, the role that risk plays in movement decisions is poorly understood.

This dissertation investigates human movement decisions under risk, exploring the rationality of movement behavior in risky constructs and whether sensitivity to risk generalizes across movements. In the first study, I compared risk-sensitivity between two continuous motor tasks (arm-reaching and whole-body leaning). Individuals were irrationally risk-seeking in both movements, and more so in whole-body leaning. In the second and third studies, I examined the effect of postural threat on discrete, risky decisions for the same motor tasks as well as for an economic task (performed while sitting and while standing). Postural threat was manipulated using an elevated platform. At ground level, individuals were again more risk-seeking in whole-body leaning than in arm-reaching. Increasing elevation only affected the task that was most salient to the threat, resulting in overweighting the probability of errors for the whole-body movement. There was no consistent effect of threat on arm-reaching, and economic choices were robust to body posture and postural threat. The first three studies establish that seemingly irrational movement behavior stems from poor estimations of motor variability and distorted utility and probability weighting, and relevant threat exacerbates irrationality. In the fourth study, I investigated whether irrationalities were also present in the valuation of effort, a predominant movement cost. I compared relative valuations of gains and losses between an effort-based movement domain and an economic domain. Individuals exhibited loss aversion in effort, suggesting that movement decisions may be geared toward avoiding higher effort over acquiring lower effort. Loss aversion was not as pronounced in this effort task as it was in equivalent financial decisions.

Ultimately, this work demonstrates that humans exhibit irrational movement decisions under risk. There is evidence that risk-sensitivity in movement generalizes, to an extent, between motor tasks, and is influenced by emotional states.

DEDICATION

To my family.

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CHAPTER 1

INTRODUCTION

Each one of our movements represents a decision-making process. Consider a number of simple, everyday movement tasks. When walking across campus to get to a meeting, we choose such factors as a walking speed, step size, and footstrike pattern. When reaching for a cup of coffee, we choose a reaching speed, grip force, arm trajectory, and hand position. There are potential costs (i.e. tripping and injuring yourself en route to the meeting, or spilling the coffee on your colleagues) and benefits (i.e. getting to the meeting on time, or enjoying a delicious sip of coffee) to the movements we make, and our motor planning choices depend on the consequences of those movements. For example, we may change the way we walk when crossing a busy street or when traversing a large patch of ice. We may reach for a cup differently when it is filled to the brim with piping-hot liquid than when it is nearly empty. The potentially injurious consequences of a poor decision compel us to investigate the mechanisms underlying this decision process.

This chapter explores previous work that underpins my dissertation. I summarize the existing literature pertaining to movement decision making under risk, including behavioral manifestations, cost quantification, neurobiological correlates, modeling techniques, and generalization studies.

1.1 Field of Study

This dissertation draws on work from the fields of neuromechanics and neuroeconomics.

Neuromechanics is an integrative science that seeks to understand the planning, coordination, and control of movement. In particular, this discipline studies interactions between the neural and musculoskeletal systems, bridging a gap between the top-down approach of neuroscience and the bottom-up approach of biomechanics to examine motor control and response. Neuromechanics spans a number of other fields, such as biology (including neuroscience, biomechanics, and physiology), engineering, robotics, mathematics, medicine, and psychology (Nishikawa et al. 2007).

Neuroeconomics is informed by research in the parent fields of neuroscience, economics, and psychology. Neuroscience uses imaging and measurements of brain activity to infer how the brain works. Economics has produced numerous theories and computational models to analyze economic-related behavior. Combining these physiological and theoretical methods with psychological information provides a framework for characterizing and understanding human choice behavior (Camerer et al. 2005; Glimcher et al. 2008; Rangel 2008; Glimcher 2009).

Understanding how and why we move the way we do in various environments is a central problem in the study of human behavior. My research utilizes principles from neuromechanics and neuroeconomics to study decision-making in the context of movement.

1.2 Decisions Under Risk

A decision-making framework is a relatively new approach in the analysis of movement behavior and motor control. However, the general field of judgment and decision making (J/DM) has been amassing scientific attention for centuries, with notable contributions by Daniel Bernoulli (1738), William James (1884), Herbert Simon (1950s), and Amos Tversky (1970s, 1980s) and Daniel Kahneman (1970s-present day).

Research in J/DM continues to resolve the extent to which humans make rational decisions. While rationality may be defined a number of different ways, let us consider a rational decision as a choice that would be made consistently for some given amount of information and that is optimal for achieving some goal. Interestingly, humans often make decisions that violate principles of rationality. Behavioral and psychological studies have demonstrated that humans sometimes employ heuristics when making judgments, resulting in biased decisions and systematic deviations from rational behavior (Tversky and Kahneman 1973, 1974, 1983; Kahneman et al. 1991; Shafir et al. 1993; Wilson et al. 1996; Thaler 1999; Epley and Gilovich 2001; Slovic et al. 2002; Schwarz and Vaughn 2002; Kahneman and Frederick 2002). For example, imagine you are offered two choices: a 50:50 gamble of winning either \$0 or \$100, and a sure bet of \$45. The expected value of the gamble is higher than that of the sure bet (\$50 vs. \$45), but most people prefer the sure bet. Explaining and modeling these apparent irrationalities is an ongoing mission in J/DM and neuroeconomic research.

Of specific interest is how risk affects our decisions. We shall define *risk* as variance in an action's outcome. In other words, a decision made under risk means that your decision could result in a range of different outcomes. The amount of risk in an environment is affected by the values of those outcomes (where a larger range of values means higher risk) as well as the probability of achieving those outcomes (where probabilities approaching chance mean higher risk). A *risk attitude*, or *risk preference*, indicates how an individual behaves, or what kind of choices an individual makes, in the presence of risk. A risk attitude can be classified as risk-neutral, risk-seeking, or risk-averse. *Risk-sensitive* behavior specifically refers to a risk-seeking or risk-averse attitude, in which an individual is affected by risk and is not risk-neutral.

1.2.1 *Economic decisions under risk*

Within the J/DM literature, there is a wealth of research dedicated to determining human choice behavior under risk in the economic domain. The intention of this section is not to summarize the whole of this literature, but rather to point out several primary considerations and findings that can inform similar studies in the movement domain.

Recall the example of choosing between a 50:50 gamble of winning either \$0 or \$100, and a sure bet of \$45. Why do we tend to prefer the sure bet over the gamble, even though the gamble will have a higher average payoff? This phenomenon can be explained as an *aversion to risk* in monetary gains. People tend

to be less risk-averse in these monetary lottery tasks when a greater amount of money is involved. In trying to account for this risk-aversion in economic decisions, Bernoulli (1954) proposed that individuals do not evaluate money or goods by their price, but rather by a subjective valuation (utility). He suggested that utility is a concave function of money, wherein there is a larger difference in the subjective values of small monetary gains than in the difference in the subjective values of large monetary gains. However, while people tend to be risk-averse in gains (preferring a sure win of \$45 to a 50:50 gamble of winning either \$0 or \$100), they are risk-seeking in losses (preferring a 50:50 gamble of losing either \$0 or \$100 to a sure loss of \$45). And whereas utility is a concave function for gains, it is a convex function for losses; there is still a larger difference in the subjective values of small monetary losses than in the difference in the subjective values of large monetary losses. Furthermore, this utility function is steeper for losses than for gains. In what Kahneman and Tversky (1984) call “loss aversion,” people find it more aversive to lose a given amount of money than it is desirable to gain that same amount of money. Thus, the utility function for gains and losses takes an S-shaped form, as shown in Fig. 1.1.

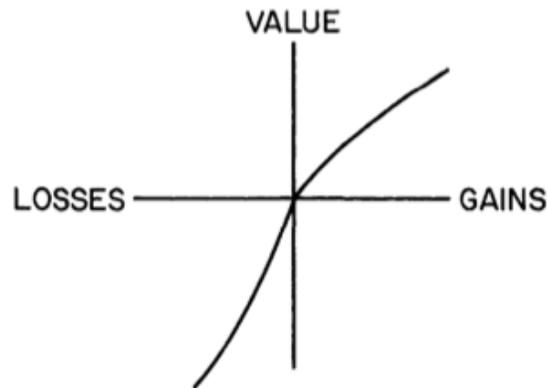


Figure 1.1. A hypothetical utility function, from Kahneman and Tversky (1984). Utility, or subjective value, is concave for monetary gains and convex for monetary losses. This function is considerably steeper for losses (loss aversion).

Human choice behavior in economic tasks has also provided evidence that the probability of receiving a gain or incurring a loss also affects how we value the gain or loss. Specifically, people tend to overweight small probabilities and underweight large probabilities (Kahneman and Tversky 1979, 1984). For gains, this means that any attractiveness of low probability events is increased while that of high probability events is reduced. For losses, any aversiveness of low probability events is increased while that of high probability events is reduced.

Together, these findings construct a so-called “fourfold pattern” of risk attitudes, confirmed with experimental data. In an economic domain, people are risk-averse for gains with large probabilities and losses with small probabilities, and they are risk-seeking for gains with small probabilities and losses with large probabilities.

1.2.2 Movement decisions under risk

Risk arises naturally in motor control. Our movements are inherently variable, meaning that we cannot make exactly the same movement twice. For example, when making repeated movements (i.e. 100 trials of pointing to a mark with your index finger), there is variability in the endpoint position, peak velocity, and acceleration profile. Movement variability stems from noise in perception, planning, and execution of a movement, as well as from noise in the encoding and transmission of neural signals (van Beers et al. 2002; van Beers et al. 2004; Churchland et al. 2006).

As in the economic domain, movement behavior also changes in the presence of risk. When deciding how to move, one must consider two important factors: movement variability and the rewards or penalties that could result from the movement. In studies of motor control, risk can be manipulated explicitly (e.g. with artificial rewards and penalties) or implicitly (e.g. with physical threat).

Risk-sensitivity in pointing and arm-reaching have been examined under several risk-related paradigms. In a rapid pointing task with explicit reward and penalty regions, Trommershäuser et al. (2003) found that subjects were approximately able to maximize their reward over many trials, indicative of *risk-neutral* motor behavior. Contrastingly, in a lottery task involving perception of endpoint accuracy in a pointing task, subjects chose a riskier lottery over a safer lottery on a majority of trials, suggesting *risk-seeking* behavior (Wu et al. 2009).

And in a continuous arm-reaching/steering task involving a tradeoff between effort and accuracy in the presence of sensorimotor noise, which is consistent with risk-averse behavior (Nagengast et al. 2010). So although these studies have specifically addressed risk-sensitivity in arm movements, there are conflicting findings of risk attitudes for the distinctly different experimental paradigms.

Studies of risky decision making during more complex movements, such as goal-directed postural control or locomotion, are less prolific. Whole-body movement behavior is often assessed through measurements of the center of pressure (COP). A body's COP is the position of its resultant ground reaction force vector. Postural threat and fear of falling modify COP control and adjustments, particularly in reduced COP displacement and velocity (Adkin et al. 2000, 2002; Brown et al. 2006; Carpenter et al. 2001, 2006; Davis et al. 2009). Or, when transitioning to a narrow pathway during walking, young adult subjects decrease their step width, and older adult subjects take faster steps compared with usual gait (Dunlap et al. 2012). Notably, no study has quantified risk-sensitivity during whole-body movements.

1.2.3 Role of affect

Studies of judgment and decision making have predominantly focused on cognitive, rather than emotional, processes. Seminal postulations of human choice behavior have assessed our proficiency in logical reasoning, for example, by examining our information-processing capabilities (Simon 1956), our reliance on heuristics and biases (Tversky and Kahneman, 1974), and our inherent strategies

for preference construction (Tversky et al. 1988). However, these works neglected the role of emotions in decision making. Damasio (1994) challenged this convention with the somatic marker hypothesis. He proposed that we build associations between the physiological state of our body and different emotions, and we learn to attribute these emotions to various stimuli or images when physiological signals (somatic markers) occur. In the brain, the ventromedial prefrontal cortex is responsible for the associations between stimuli and emotions. The somatic marker hypothesis is supported by various behaviors of patients with damage to the ventromedial prefrontal cortex. Unlike healthy individuals, these patients exhibited no change in skin conductance response when shown emotionally charged visual images. They also perform poorly in a card-based gambling task, choosing a high-risk strategy in spite of repeated losses (Bechara et al. 1994). Damasio concluded that both cognitive and emotional processes help us make decisions, and somatic markers may simplify decision making by directing (or biasing) our choices.

In recent decades, a two-system, or dual-process, model of judgment and decision making has garnered much interest. This model distinguishes a decision process based on intuition (System 1) from one based on reasoning (System 2). While System 1 is fast, automatic, associative, and emotion-based, System 2 is slow, analytic, flexible, and rule-based (Epstein 1994, Sloman 1996, Stanovich and West 2002, Kahneman 2003, among others). The two-system model can also explain how humans cope with risk in the modern world. We can have an intuitive, visceral reaction (risk as feelings, associated with System 1) or a systematic, deliberative

evaluation (risk as analysis, associated with System 2) (Slovic et al. 2004). The interaction and relative contributions of these systems is critical to how we make decisions, and, ultimately, whether these decisions are rational.

Let us now consider a primary characteristic of System 1: affect. Slovic (2002) uses the term affect to mean the “goodness” or “badness” that is (a) experienced as a state of feeling (e.g. happiness or sadness) and is (b) associated with a stimulus (e.g. the stimulus is viewed positively or negatively). Slovic also uses the phrase “affect heuristic” to characterize our reliance on feelings in guiding or informing the decision-making process. Affect can directly motivate our behavior, as good/pleasant feelings drive us toward choices that may reproduce those feelings, and bad/unpleasant feelings drive us toward choices that may prevent or avoid those feelings.

Affect can also influence our judgments and perceptions of risk, as our feelings about an event cause us to perceive the risks and benefits of that event differently. That is, an event that elicits good/favorable feelings is judged as having low risk and high benefits, whereas one that elicits bad/unfavorable feelings is judged as having high risk and low benefits (Finucane et al. 2000). Specific emotions can have different effects on our judgments of risk. Interestingly, fear and anger seem to have opposing effects on our perception of risk: while fear is associated with perceptions of uncertainty and situational control, anger is associated with perceptions of certainty and individual control. This means that fear and anger can be related to pessimistic and optimistic assessments of risk,

respectively (Lerner and Keltner, 2000). Furthermore, events that carry strong affective meaning are often perceived as more or less likely than they actually are. For example, people's feelings about winning the lottery are similar whether the probability of winning is 1 in 10 million or 1 in 10 thousand. Thus, in the presence of risk or uncertainty, emotions about an affect-rich event may have an all-or-none characteristic, so we are insensitive to probability. That is, feelings are more sensitive to the *possibility* of an event than the *probability* of its consequences (Loewenstein et al. 2001). But affect not only shapes our own perceptions of risk; it may also impact how we perceive others' attitudes toward risk. In predicting other people's choices under risk, subjects predict that others' choices are systematically regressed (more risk-neutral) from their own. That is, a risk-seeking individual predicts others will be also risk-seeking, but less so. A risk-averse individual predicts others will also be risk-averse, but less so.

Affect has also been shown to alter our movements. Emotionally charged visual stimuli (e.g. pleasant or unpleasant images) can reduce reaction time (Flykt 2006) and increase force production (Coombes et al. 2008, Schmidt et al. 2009). When force production must be held constant despite changes in emotional state, subjects show increased brain activity in the dorsomedial prefrontal cortex (dmPFC). To maintain this constant force output during emotional changes, subjects seem to engage a functional circuit between the dmPFC and premotor cortex, indicating that the premotor cortex, previously associated with motor planning and execution, is also involved in controlling movement in emotional

contexts (Coombes et al. 2012). During quiet upright stance, subjects who imagined themselves in a painful situation (with visual emotional stimuli) exhibited decreased COP displacements, higher tibialis anterior activity, and higher variability in soleus activity compared with subjects who imaged themselves in a non-painful situation (Lelard et al. 2013). As with our judgments, emotion can prime our motor behavior to approach pleasant stimuli or avoid unpleasant stimuli. In studies of upper arm flexion and extension, subjects are quicker to push a lever than to pull it when shown a negative stimulus, and they are quicker to pull a lever than to push it when shown a positive stimulus (Chen and Bargh 1999, Duckworth et al. 2002). During gait initiation, a purely approach-oriented task, unpleasant visual stimuli reduces reaction time and the initial motor response, whereas pleasant visual stimuli facilitates the forward initiation of gait, manifested by increases in the velocity of anticipatory COP adjustments and the velocity of the first step (Naugle et al. 2011). An individual's mood can also affect overall gait pattern. Sad moods and depression are characterized in gait by reduced walking speeds, arm swinging, and head movements as well as greater lateral sway and more slumping posture than those with a positive mood (Michalak et al. 2009).

Although we do not yet understand the degree to which humans rely on affect in various decision-making contexts (e.g. judgment, risk perception, motor tasks), it is clear that affect plays a complex and undeniable role in behavior and mechanisms of choice.

1.3 Movement Rewards and Costs

Economic decisions and movement decisions under risk both seek to maximize rewards and minimize costs. In the economic domain, potential gains and losses of money or commodities are, appropriately, the rewards and costs to be considered when making a decision. In the movement domain, several possible rewards and costs have been proposed that the central nervous system (CNS) may be evaluating throughout the movement selection and control processes.

Movement rewards are generally tied to task goals. In goal-directed motor tasks, target acquisition signifies a successful movement, so the implicit reward would be coupled with the inverse of endpoint error. Explicit rewards and penalties, such as point scores or financial compensation, are also imposed in movement tasks to designate successful movements (Trommershauser et al. 2003, 2005, 2006; Wu et al. 2009, 2011; Shmuelof et al. 2012; Dam et al. 2013).

The predominant implicit cost in movement is effort. Formally, effort refers to the metabolic energy required to perform a given movement. Metabolic energy expenditure during movement can be measured directly (using a calorimeter) or indirectly (such as in expired gas analysis, which tracks the rates of oxygen consumption and carbon dioxide production). Although metabolic cost provides an direct, objective measure of effort, these measurements are difficult to make since they require specialized equipment and highly-controlled experiments. Other signals, such as force, muscle activity, and rate of torque development are often

used as proxies for effort (Nelson 1983; Emken et al. 2007; Franklin et al. 2008; Kistemaker et al. 2010; de Rugy et al. 2012; Berniker et al. 2013). Care should be taken when employing these signals as effort costs as they can deviate significantly from metabolic measurements (Huang et al. 2012).

Minimization of effort has been used to explain a wide range of movement behavior in locomotion and arm-reaching. For example, preferred walking speed aligns with a metabolic minimum (Alexander 1989). Huang et al. (2012) were the first to measure metabolic cost during reaching movements; they reported a distinct metabolic reduction during the motor learning process. Optimization of movement time and energy expenditure can account for the typical undershooting of targets observed in reaching (Lyons et al. 2006) Increasing motor effort can also discount rewards (Prevost et al. 2010; Hartmann et al. 2013) or reduce changes of mind in a reaching task with uncertainty (Burk et al. 2014). Intriguingly, it appears that minimization of effort is more important than minimization of motor variability, another potential movement cost. O'Sullivan et al. (2009) dissociated the two costs using a force-production coordination task; they discovered that importance of effort (here, quantified as a sum of squared motor commands) outweighed variability by a factor of seven.

Importantly, there are widespread demonstrations of irrationality in economic decision making under risk, which is often traced to distortions in the utility function – specifically, diminishing sensitivity and gain/loss asymmetry (loss

aversion). A remaining question is whether the rewards and costs in movement decisions suffer from similar distortions.

1.4 Neural Mechanisms of Decisions Under Risk

Over the past few years, we have achieved a significantly better understanding of how the brain makes decisions. Functional magnetic resonance imaging (fMRI) is a common neurometric tool used to examine the neural structure pathways involved in various decision-making contexts.

Recent studies of primate choice mechanisms suggest that we use a two-stage neurobiological process to guide decision making. The first stage is one of valuation, wherein the values of actions or goods are learned and represented in the basal ganglia and frontal cortex. The second stage is one of selection, as various regions of the brain such as the posterior parietal cortex (PPC) and movement-related areas perform a “winner-takes-all” operation on these values to choose among the actions or goods (Glimcher 2009). Although we cannot yet specify all neural pathways that contribute critically to choice, the hypothesized two-stage model is supported by neuronal recordings from animal in psychophysical tasks (Newsome et al. 1990; Gold and Shadlen, 2007) as well as in movement control (Platt and Glimcher 1999; Glimcher 2002; Wunderlich et al. 2009).

An alternative hypothesis, known as a multiple-self model, is that choice behavior results from the interaction between two competing neural systems. Such

models propose that there are two primarily independent systems at odds during the decision-making process: one associated with emotional subregions of the brain and the other associated with the rational subregions. For example, McClure et al. (2004) suggest that the emotional system is formed by the basal ganglia and medial prefrontal cortex (mPFC), and the rational system is comprised of the posterior parietal cortex and the dorsolateral prefrontal cortex. However, these models are not well supported by neurobiological data (summarized in Glimcher et al. 2009).

Many regions in the brain are responsible for encoding various decision-making parameters. Some parameters may be formed in separate, distinct brain regions, while others may be computed using more than one region. For example, in an economic task, Tobler et al. (2007) concluded that expected value is represented in the striatum and parts of the frontal cortex, whereas reward uncertainty is rendered separately in the orbitofrontal cortex (OFC). Risk modifies neural activity, as seen when increasing uncertainty of a visual stimulus affected coding of expected value signals in the lateral prefrontal cortex (Tobler et al. 2009). The OFC is also involved in coding stimulus values in variety of contexts, whereas the anterior cingulate cortex (ACC) and the supplementary motor area contribute to coding action values (reviewed in Rangel and Hare 2010). Activity in ventral striatum been repeatedly shown to correlate with rewards and punishments (Chib et al. 2012). Observing another person's actions that lead to monetary rewards and punishments can modulate electroencephalography (EEG) activity in the motor cortex, and this activity is greater for rewards than punishments. (Brown et al. 2013).

When comparing risk preferences across different reward types (money, food and water), Levy and Glimcher (2011) found that the ventromedial prefrontal cortex (vmPFC) is responsible for representing subjective values of these rewards on a common scale for direct comparison, and the same structure has shown activity in multi-effector action selection (Madlon-Kay et al. 2013). When comparing risk preferences between dissimilar decision-making domains (an economic task and a motor task, both with monetary rewards), Wu et al. (2011) found that the medial prefrontal cortex (mPFC) and the posterior cingulate cortex (PCC) represented subjective utility of money for both domains. The mPFC also coded probability of outcomes for both domains.

Doya (2008) summarizes many neural structures and chemicals involved in valuation and decision through a concise table. Although significant progress has been made in identifying these structures and determining their roles in the decision-making process, we still have much to learn about the neurobiology of making choices under risk, in movement and in other domains. It is particularly unclear what computational mechanisms are employed by the brain to arrive at theoretical and action-based decisions.

1.5 Modeling

A number of models have been proposed to explain or predict decision making under risk. These models may be normative (identifying the best, or optimal,

decision to make) or descriptive (determining what decision someone would actually make, regardless of whether it is optimal or not).

Because our movements are inherently variable, a statistical framework is often used to examine movement decision making. There are a number of models that are formulated based on the statistical nature of choices under risk, such as Bayesian decision theory, prospect theory and cumulative prospect theory, models that maximize expected gain, and various optimal control algorithms. In this section, I describe each of these model classes in turn and their applications to decisions under risk.

1.5.1 Bayesian decision theory

Wolpert and Landy (2012) conceptualize the Bayesian approach to decision making under risk with a simple, concrete example: imagine you are sitting down at a dinner party when you accidentally bump the table. Out of the corner of your eye, you think you see a wine glass tipping over. What action do you take? If you choose to make a movement to catch the glass, you still must decide on many aspects of the movement plan, such as which hand to move, where to move it, what grasp to adopt, and how to continue the movement if you manage to catch the glass. Bayesian decision theory assumes that the optimal choice depends on (1) your prior knowledge, (2) uncertainty in the available information, (3) uncertainty in the outcome of an action, and (4) the costs and benefits of an outcome. The interaction of these elements affects the choice of a movement plan. For the tipping wine glass,

you may have prior knowledge about the location of the wine glass and how full it is, as well as the typical behavior of a wine glass when it tips over (which gives you an idea of the time constraint). Since the wine glass is in your periphery, there is uncertainty regarding its location and how fast it is tipping. There is also uncertainty in your movement due to variability. Finally, there are costs (e.g. failing to catch the glass and splashing wine on the tablecloth or dinner companions) and benefits (e.g. catching the glass and being able to drink any unspilled wine) to your actions.

The hallmark of Bayesian approaches to movement planning and control is combining prior knowledge (simply called the “prior”) of the probability of the body state and environment with uncertainty in the available sensory information and in the movement outcome. Using these models, it has been shown that subjects rely more heavily on the prior when there is higher uncertainty in sensory feedback (Körding and Wolpert 2004a).

In a Bayesian framework, suboptimal movements can occur if a subject does not accurately estimate the prior (Wolpert and Landy 2012). A recent model has incorporated distorted weightings of probability, similar to cumulative prospect theory (described in section 1.4.3), into a Bayesian formulation (Fennell and Baddeley 2012)

1.5.2 Maximizing Expected Gain in Movement (MEGaMove)

Sensorimotor variability plays a large part in movement control, since a given intended action does not always lead to the same outcome (Hamilton et al. 2004; Churchland et al. 2006). A movement task should be formulated in statistical terms: we must combine the probability of the outcome (variability) and the value associated with the outcome to come up with an optimal solution for how to move (Trommershauser et al. 2003).

A well-studied task involves subjects making rapid pointing movements to overlapping, circular targets on a screen with point rewards or penalties (Trommershauser et al. 2003, 2005, 2006, 2008; Maloney et al. 2007). These authors formulated a movement-planning model that **Maximizes Expected Gain** in the selection of **Movement** strategies (MEGaMove). For a given movement task, the MEGaMove model assesses each possible movement strategy and calculates the expected gain $\Gamma(S)$ of that strategy. Expected gain is a weighted sum of the rewards associated with the successful completion of that strategy, where the weights are probabilities of achieving those rewards. In Trommershauser et al.'s pointing task with reward and penalty targets, the expected gain $\Gamma(S)$ of choosing movement strategy S throughout N trials is

$$\Gamma(S) = \sum_{i=1}^N G_i P(R_i|S) ,$$

where G_i is the reward or penalty associated with moving to a region i , and $P(R_i|S)$ is the probability of hitting that region. These probabilities are computed based on a subject's movement endpoint variability. The optimal motor action is then the action that would maximize a subject's expected gain. Subjects' actual movement endpoint behavior in a pointing task with reward and penalty circles was well-correlated with MEGaMove model predictions, suggesting that subjects were able to estimate and internalize their own movement variability and select the optimal motor plan based on the extrinsic costs of the pointing task. MEGaMove can also be formulated to minimize expected loss (Trommershauser et al. 2003).

While the MEGaMove model predicts the optimal endpoint for a motor strategy, it does not provide any details about the trajectory of a movement. Optimal control modeling is another technique that can be used to obtain information about optimal behavior in a continuous task.

1.5.3 Optimal control

Optimal control models provide an elegant mathematical framework to transform symbolic, high-level tasks (e.g. take a sip of coffee) into low-level details required by the motor system (e.g. determine the muscle activation patterns, joint rotations, and hand trajectory to reach for your coffee cup, grab it, and bring it to your lips). These models compare the control policies that would be required by different actions and select the policy that minimizes some cost function. Consider the task of reaching for your coffee cup: there are an infinite number of trajectories

along which you could move your hand to complete this task, so which one do you choose? Furthermore, when we choose a trajectory, we can move along it using infinitely many combinations of muscle activation patterns, joint angles, and velocity profiles. Optimal control models can be built to determine all of these factors; they choose movement patterns and motor control strategies that are optimal for the given task.

An optimal control model is comprised of a set of equations describing the system dynamics, control policies, and a cost function. Optimal controllers can be open-loop (feedforward) or closed-loop (feedback). Many classic models in motor control are open-loop, calculating the optimal or desired trajectory and movement parameters without accounting for online sensory feedback (Flash and Hogan 1985; Uno et al. 1989; Harris and Wolpert 1998, among others). While this approach has been shown to accurately predict some movement behaviors over time, they cannot compensate for real-time changes acting on the system, and, without feedback, cannot determine whether the desired goal has been met. On the other hand, closed-loop models, or optimal feedback control models, integrate sensory and motor noise in their representation of the biomechanical system. These models are continuously estimating and adjusting the movement strategy, and they are more successful in modeling the flexibility and variability in human movement (Loeb 1990; Kuo 1995; Todorov and Jordan 2002, among others).

Optimal controllers select and execute the movement that minimizes a cost (or value) function. Various cost functions have been proposed for different

movement tasks; for example, it has been suggested that the CNS chooses motor strategies that minimize smoothness of the trajectory (Flash and Hogan 1985), joint torques (Uno et al. 1989), or variance due to signal-dependent noise (Harris and Wolpert 1998; Todorov and Jordan 2002). Importantly, many such studies assume a cost function and compare observed subject behavior with that predicted by the model, rather than directly measure the cost function. Alternatively, cost functions in sensorimotor learning (Körding and Wolpert 2004b) and force production (Körding et al. 2004) have been inferred using model fitting or subject-specific “indifference lines,” where different costs are valued equally. Several risk-sensitive cost functions have been offered to generate controllers that are more descriptive of human behavior (Whittle 1981; Nagengast et al. 2010; Medina et al. 2012a, 2012b; Grau-Moya et al. 2012). Accurate construction of the cost function is critical in characterizing and predicting movement behavior, and the form and weighting of the components in these functions remains an open problem in motor control.

Overall, optimal control models are complex but well suited for the analysis of goal-directed movements, which inherently possess stochasticity (e.g. sensorimotor noise) and can possess nonlinearity (e.g. stability limits in postural control). This approach can offer a richer description of the mechanisms underlying movement than models of discrete motor behavior, such as MEGaMove.

1.5.4 Prospect theory

Prospect theory was proposed by Tversky and Kahneman (1979) as an alternative to expected utility theory (EUT) in describing decision making under risk. Whereas EUT had been accepted as a normative model of rational choice, prospect theory was developed to explain a variety of human choice patterns that directly violate EUT. An updated model of prospect theory, called cumulative prospect theory (CPT), ultimately argues that these deviations from optimal, or rational, behavior results from distorted valuation of the rewards/costs and distorted weighting of probabilities associated with an outcome. Specifically, these models suggest that individuals harbor nonlinear representations between the actual value of an outcome and the subjective value, and between the probability of an outcome and the subjective weight associated with that probability (Tversky and Kahneman 1979). The CPT framework is commonly used to assess risk attitudes and choice behavior through quantification of these distorted weightings (Wu and Gonzalez 1996; Neilson and Stowe 2002; Wu et al. 2009, 2011; Glaser et al. 2012)

Recent works have also discussed the role of emotions in the context of decision making models, particularly in prospect theory. Affect-rich and affect-poor situations may alter our perceptions of value or probability of an outcome. Rottenstreich and Hsee (2001) proposed an affect-reliant shape of the probability weighting function, with affect-rich events creating a more S-shaped curve than affect-poor events. These authors later suggested that affect could also change subject valuation (Hsee and Rottenstreich 2004).

Ultimately, the quantitative framework of CPT offers promise for examining many areas of human motor decision making. It also allows us to compare decision making and the representation of value and uncertainty across multiple populations, contexts, and task domains and to elucidate generalizable principles.

1.5.5 How effective are these models?

Despite advancements in the aforementioned modeling strategies, we must perpetually ask ourselves to what degree these models reflect true human behavior. The interaction between an organism, its needs, and its environment can be complex, dynamic, and difficult to quantify. This may be evident not only to an experimenter trying to identify various mechanisms of choice, but also to the organism that is making a choice. Simon (1956) argued that organisms might behave in a “satisficing” manner rather than an optimal one. A satisficing strategy is one that provides some specified level of satisfaction for all of an organism’s needs. Simon proposed a rational model of behavior for a simple-minded organism (e.g. a rat) in a survival scenario. Given limited access to information and limited capacity for neural computations, an organism’s observed choice behaviors may result from a simplified set of choice mechanisms that appear approximately rational. His model is strikingly different than previous economic models in that it does not rely on a utility function or a marginal rate of substitution (the rate at which you are willing to exchange one good for another), thusly demonstrating that an organism can satisfy various needs without employing an elaborate means of

choosing among them. This suggests that some skepticism is warranted toward postulations of sophisticated decision-making mechanisms in humans. Camerer (1989) similarly warns that no theory can explain all choice data, and though the generalization of decision theories is a tempting enterprise, it is possibly unproductive in the long term. However, models that capture such choice regularities as gain-loss asymmetry and nonlinear probability weighting may provide sufficient descriptions of decision making under risk (Camerer 1989; Wu and Gonzalez 1996). With this in mind, let us now further explore empirical findings of the generalizability of risk preferences in a variety of decision contexts.

1.6 Generalization of Risk Attitudes

1.6.1 Demonstrations of differing risk attitudes across domains

A number of studies have found that risk attitudes are highly domain-specific. Weber et al. (2002) used a psychometric scale to assess risk-seeking behavior in five different domains: financial, health/safety, recreational, ethical, and social decisions. The authors found that individuals' risk attitudes were not consistently risk-seeking or risk-averse across the five domains, and that the degree of risk-seeking behavior was associated with the perceived benefits and risk of an activity. Additionally, there is evidence that individual risk attitudes in these five domains are correlated with broad personality dimensions (Weller and Tikir 2010).

Wu et al. (2009, 2011) compared subjects' risk attitudes in an economic lottery task with those in an equivalent motor lottery task. They found that subjects were more risk-seeking in the motor task than in the economic. By fitting subject choices to a CPT model, they concluded that although subjects weighted rewards similarly in these tasks, they had markedly different probability weightings between the two domains. Specifically, while they tended to overweight small probabilities and underweight large probabilities in the economic task, consistent with findings in other economic studies, they showed the opposite pattern of distortion in the motor task.

1.6.2 Demonstrations of similar risk attitudes across domains

Levy and Glimcher (2011) compared the valuation of monetary rewards with that of primary rewards (e.g. food and water). These authors noted that although the human brain evolved to make choices regarding primary rewards, modern studies often investigate risk preferences toward money. Naturally, this raises the question of whether the brain uses a common scale to represent the values of these different reward types. Food- and water-deprived subjects made choices between same-type and mixed-type lotteries. Although individuals exhibited idiosyncratic risk preferences, within-subject preferences across these reward types were highly correlated. That is, a subject that was more risk-averse in one of these reward types was likely to be more risk-averse in the other reward types. These authors conclude that, when a common procedure is used to compare risk attitudes across differing

domains, individual risk attitude in one reward type (such as money) may predict attitude for other rewards (such as food and water).

1.6.3 Altering individual risk attitudes

A recent study indicates that it is possible to modify our risk attitudes in one domain by encouraging a certain attitude in a different domain. Verbruggen et al. (2012) examined the effect of multitasking on risk behavior: specifically, at the interaction between motor control and gambling. They found that inducing cautiousness in a motor task (“stopping” before hitting a computer key) reduced risky betting in a simultaneous gambling task. Furthermore, training in this cautious motor task could produce risk-averse gambling behavior for up to two hours. These results suggest that inhibitory motor processes overlap with risk-aversion in monetary decision making, and risk preferences in some tasks may be altered by exploiting different executive control systems.

CHAPTER 2

THESIS OBJECTIVES

Through a review of the current literature on motor control under risk, I have presented advancements in explaining movement decisions in various risky environments. This chapter establishes the motivation, specific aims, and significance of my thesis work.

2.1 Motivation

At present, there is a significant gap in our existing knowledge of movement-based decision making. It remains unclear whether humans make rational decisions in movement under risk. That is, do people appropriately account for their variability and for the reward/penalty outcomes during movement? Furthermore, though we may be able to determine an individual's risk preferences in a specific movement task, we cannot draw meaningful conclusions about this individual's behavior under risk in other movement tasks or environments. It is possible that risk attitudes are highly subject-specific and context-dependent. That is, a subject may exhibit risk-seeking behavior in one task and risk-averse behavior in a different task. This work aims to extend our knowledge of movement decision making under risk by examining the generalization of individual risk preferences. We will directly confront the conflicting accounts of risk-sensitivity by quantifying

subject-specific changes in risk responses for different movements and environments.

2.2 Specific Aims

The main objective of this research is to examine the rationality of movement decisions under risk and whether movement preferences generalize to other settings. I will address four specific aims in my dissertation:

AIM 1: Quantify movement risk-sensitivity across various risky environments, and compare behavior between two dissimilar movements.

AIM 2: Establish the effect of postural threat on movement decisions under risk, and compare behavior between two movements possessing different pertinence to the threat.

AIM 3: Establish the effect of postural threat on economic decisions under risk, when the threat is not salient to the decision task.

AIM 4: Examine the presence of loss aversion (the desire to avoid losses more strongly than the desire to acquire gains) in effort-based movement decisions, and determine whether loss aversion in economic decisions generalizes to movement effort.

2.3 Significance

My dissertation work provides crucial advancements in understanding movement decision making under risk. This research showcases the first comparison of risk attitudes across different movement tasks and emotional states, extends our knowledge of risk preferences across motor and non-motor domains, and introduces analyses of loss aversion in movement effort, a predominant movement cost. Results will help determine whether there are generalizable principles such that movement decision making in one context can be predicted and trained using decision making tasks in other contexts. This would be advantageous as some tests of decision making under risk, such as economic choices, are more amenable to implementation and evaluation outside a laboratory environment. Fundamentally, these findings are applicable to a number of other research fields that involve movement and risk, such as rehabilitation, sports, and military practices.

2.4 Outline

The remainder of this document is organized into five chapters.

- Chapter 3 describes an experiment investigating movement decisions in a continuous task with implicit risk. Risk-sensitivity is compared between two movements (arm-reaching vs. whole-body leaning).

- Chapter 4 describes an experiment investigating the effects of postural threat on movement decisions in a discrete task with implicit risk. Risk-sensitivity is compared between two movements (arm-reaching vs. whole-body leaning) and two conditions of threat (low elevation vs. high elevation). Here, the postural threat is potentially salient to the decisions under risk.
- Chapter 5 describes an experiment investigating the effects of body posture and postural threat on economic decisions in a discrete task with explicit risk. Risk-sensitivity is compared between two body postures (sitting vs. standing) and two conditions of threat (low elevation vs. high elevation). In this case, the postural threat is not salient to the decisions under risk.
- Chapter 6 describes an experiment investigating effort-based movement decisions in a discrete task with explicit risk. Decreases in effort are framed as gains and increases in effort are framed as losses to examine loss aversion in effort. Loss aversion is compared between two domains (effort vs. economic).
- Chapter 7 summarizes the main findings of this thesis, discusses their implications, and proposes future directions.

CHAPTER 3

THE EFFECT OF MOVEMENT TASK ON RISK-SENSITIVITY

The work in this chapter is also published as: O'Brien MK, Ahmed AA. Does risk-sensitivity transfer across movements? *Journal of Neurophysiology* 109: 1866–1875, 2013.

3.1 Abstract

An intriguing finding in motor control studies is the marked effect of risk on movement decision making. However, there are inconsistent reports of risk-sensitivity across different movements and tasks, with both risk-seeking and risk-averse behavior observed. This raises the question of whether risk-sensitivity in movement decision making is context-dependent and specific to the movement or task being performed. Here, we investigated whether risk-sensitivity transfers between dissimilar movements within a single task. Healthy young adults made arm-reaching movements or whole-body leaning movements to move a cursor as close to the edge of a virtual cliff as possible without moving beyond the edge. They received points based on the cursor's final proximity to the cliff edge. Risk was manipulated by increasing the point penalty associated with the cliff region and/or adding Gaussian noise to the cursor. We compared subjects' movement endpoints to endpoints predicted by a subject-specific, risk-neutral model of movement planning. Subjects demonstrated risk-seeking behavior in both movements that was

consistent across risk environments, moving closer to the cliff than the model predicted. However, subjects were significantly more risk-seeking in whole-body movements. Our results present the first evidence of risk-sensitivity in whole-body movements. They also demonstrate that the direction of risk-sensitivity (i.e. risk-seeking or risk-averse) is similar between arm-reaching and whole-body movements, although degree of risk-sensitivity did not transfer from one movement to another. This finding has important implications for the ability of quantitative descriptions of decision making to generalize across movements and, ultimately, decision-making contexts.

3.2 Introduction

Each one of our movements represents a decision made under risk. The potentially injurious consequences of a poor decision compel us to investigate the mechanisms underlying the decision process. This process is partly determined by our sensitivity to risk, i.e., whether one is risk-seeking or risk-averse. However, it remains unclear whether an individual maintains the same risk-sensitivity across movements. Will a risk-averse skier also be risk-averse when they golf? Can we recover an individual's risk-sensitivity in one task by simply observing their behavior in another?

A statistical framework is often used to examine movement decision making in a variety of tasks that involve risk (van Beers et al. 2002; Faisal et al. 2008;

Trommershäuser et al. 2003, 2008). Models of optimal movement planning determine how an individual should behave to maximize expected reward, accounting for extrinsic costs and sensorimotor variability. In past studies, these models have correctly predicted the behavior of human subjects in goal-directed pointing movements with a symmetric expected gain landscape. This suggests that subjects performed optimally in these movements, accurately internalizing their own sensorimotor variability and additional task-related costs (Trommershäuser et al. 2003). The high degree of optimality also indicates that subjects adopted a *risk-neutral* attitude during this motor task (Braun et al. 2011). In other words, they were not sensitive to the environmental risk, defined here as the variance over potential outcomes. Contrastingly, risk-sensitive behavior may emerge if an individual considers both risk and return when deciding how to act, such as proposed by Markowitz (1952) in a financial setting. An individual may also manifest risk-sensitivity if he is unable to appropriately evaluate the reward structure of the task (distorted utility weighting) or if he has a skewed weighting of his sensorimotor variability (distorted probability weighting). Other movement studies have found evidence of *risk-seeking* behavior (Wu et al. 2009) or *risk-averse* behavior (Nagengast et al. 2010). However, this previous work has examined different types of movement (pointing, arm-reaching) in a variety of experimental paradigms, has not always provided feedback immediately after the movement, and has involved comparisons between subjects. Here, we investigate movement decisions in a single paradigm, providing the same form of feedback but with two

different movements to determine whether risk-sensitivity transfers from one type of movement to another.

The two movements we chose to compare were arm-reaching and whole-body leaning movements. While many studies examine arm-reaching, risk is arguably more relevant to whole-body movements. Furthermore, goal-directed whole-body movements are less familiar than arm-reaching. If risk-sensitivity transferred between movements, this would be a strong demonstration of generalization. If risk-sensitivity did not transfer, this would establish its dependence on movement context.

We designed an experiment to investigate risk-sensitivity in arm-reaching and whole-body movements. We manipulated risk in the form of point penalties and/or sensorimotor variability, thereby allowing us to examine the consistency of movement decisions across various risk environments and to determine whether underlying risk-sensitivity arises from distortions in utility or probability. We hypothesized that subjects would demonstrate risk-sensitive behavior in both movement tasks, and that direction and degree of risk-sensitivity would transfer between the tasks. That is, if a subject was risk-seeking in arm-reaching, we expected them to be equally risk-seeking in the whole-body task. Our findings may advance an understanding of whether risk-sensitivity in one context can predict movement behavior in other contexts.

3.3 Materials and Methods

We examined a paradigm in which subjects guided a cursor toward the edge of a virtual cliff using either arm-reaching movements or whole-body leaning movements. Risk was manipulated experimentally in a series of conditions by increasing point penalties and/or task-relevant cursor variability, and subject performance was compared with estimates of a risk-neutral movement planner. Such comparisons allow us to quantify an individual's risk-sensitivity based on their own sensorimotor variability and experimentally-imposed risk. Manipulating risk in this task enables us to examine the consistency of the *direction* and *degree* of risk-sensitivity. The *direction* of risk-sensitivity refers to the classification of behavior as risk-neutral, risk-seeking, or risk-averse. The *degree* of risk-sensitivity refers to the strength, or magnitude, of this preference.

Subjects

Twenty right-handed, healthy subjects (12 males, 8 females; mean age, 23.9 ± 2.6 years) participated in both an arm-reaching and a whole-body movement task. All subjects provided informed consent, and the experimental protocol was approved by the Institutional Review Board of the University of Colorado Boulder.

Experimental protocol

In the arm-reaching experiment (ARM task), subjects used their dominant arm to grasp the handle of a robotic manipulandum (Interactive Motion Technologies Shoulder-Elbow Robot 2) and drive a cursor to the edge of a virtual cliff. In the whole-body experiment (WB task), subjects stood on a forceplate (AMTI LG-4-6-1) and used their center of pressure to move the cursor to the cliff edge. A monitor mounted in front of the subject displayed a cursor, a starting position, and penalty region (cliff) set at two-thirds of the subject's maximum movement distance, as shown in Figure 3.1. To determine the maximum movement distance, we asked subjects to reach or lean as far forward as they could, and we used the maximum value of three attempts. For the ARM task, subjects were seated and secured with a 4-point seatbelt, which prevented rotation of the shoulders or trunk during reaching. For the WB task, subjects wore socks and stood with their feet shoulder-width apart; they also kept their heels in contact with the forceplate and their arms crossed in front of their chest. Visual feedback of the arm or body was not intentionally obscured in any way.

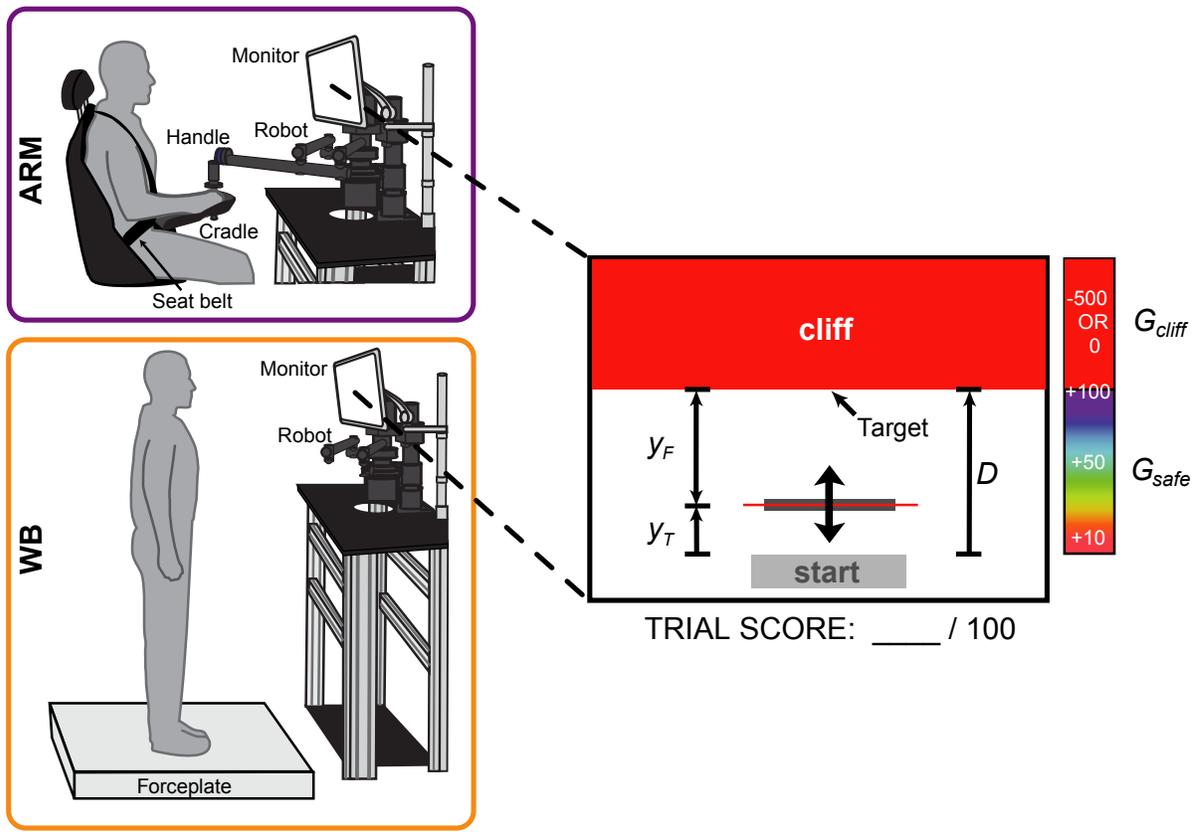


Figure 3.1. Experimental setup for ARM and WB tasks. (Left) Schematic of arm-reaching (ARM) and whole-body (WB) movement tasks. (Right) Visual feedback of cliff paradigm includes starting position, rectangular cursor, and cliff. Arrow indicates direction of cursor movement. Cursor endpoint determines trial score, either G_{safe} or G_{cliff} . Endpoints are denoted as y_T when referring to a distance traveled *toward* the cliff and as y_F when referring to a distance *from* the cliff. The cliff distance D is set at two-thirds of the subject’s maximum movement distance.

We created small visual distinctions between the ARM and WB experiments to encourage subjects to formulate movement strategies independently for each task. One such distinction was the shape of the cursor: in the ARM task, the cursor was a circle of radius 0.25-cm, whereas in the WB task, the cursor was a 0.25x2-cm rectangle. Since maximum center of pressure movements are inherently smaller

than maximum arm-reaching distances, cursor feedback was scaled 2:1 in the WB task. Furthermore, the cliff was not located at the same place on the screen in the ARM and WB experiments to ensure that subjects did not simply aim for the same point on the screen during each movement. The order of movement tasks was varied across subjects. Eleven of the 20 subjects performed the ARM task first followed by the WB task.

Subjects were instructed to make a swift out-and-back movement to rapidly move the cursor as close to the edge of the cliff as possible without going into the cliff region and rapidly return to their starting position. They received a point score for each trial based on the cursor's maximum excursion to the cliff edge. On the safe side of the cliff, points were awarded as a linear function of movement distance (G_{safe}), and the maximum possible score of 100 points was associated with moving the center of the cursor perfectly to the edge of the cliff. A different score (G_{cliff} , either 0 points or -500 points) was given if the cursor crossed the cliff edge at any time. Before each trial, the subject had to center the cursor in the starting position, and an auditory tone signaled the beginning of a trial. During a trial, the cursor was constrained to move toward and away from the cliff, which corresponded to the subject's anteroposterior direction. In both tasks, cursor movement was one-dimensional and unaffected by side-to-side movement of the arm or center of pressure. Subjects were given 800 milliseconds to complete a trial, and the movement endpoint was taken as the maximum distance moved toward the cliff from the starting position. We imposed this short trial length to discourage subjects

from “hovering” near the cliff region and making small adjustments to increase their scores. Rather, subjects had to make a quick movement decision and return to the starting position.

Subjects completed this paradigm under various risky environments. Risk was manipulated by increasing sensorimotor variability and/or point penalties. We tested four risk conditions for each movement task, with 120 trials performed for each condition: (1) NULL, where there was no point reward nor penalty ($G_{\text{cliff}} = 0$ points) for entering the cliff region; (2) NOISE, where Gaussian noise (with standard deviation $\sigma_N = 0.3\text{cm}$) was added to the cursor position in the direction of movement; (3) CLIFF, where a penalty ($G_{\text{cliff}} = -500$ points) was incurred for moving into the cliff region; (4) CLIFF+NOISE, where both the large point penalty and Gaussian noise were included. Adding noise to the cursor and applying a large penalty to the cliff region corresponds to increasing risk by increasing the variability and penalty associated with the movement task, respectively. Thus, the tasks are categorized as low-penalty and low-variability for NULL, low-penalty and high-variability for NOISE, high-penalty and low-variability for CLIFF, and high-penalty and high-variability for CLIFF+NOISE. The cursor noise was perceivable to the eye and was applied for the duration of the out-and-back movement. Subjects also received verbal instructions before each condition describing the value of the cliff penalty. Twelve subjects performed the conditions in the above order (NULL, NOISE, CLIFF, CLIFF+NOISE). To determine whether the order of conditions

affected risk-sensitivity, eight subjects performed these conditions in a randomized order.

Variability testing

We determined each subject's sensorimotor variability as a function of movement distance in a separate experiment. Here, we measured each subject's endpoint variability at five discrete distances: 20-, 40-, 60-, and 80-percent of their maximum movement, as well as the distance to the cliff edge (66-percent), with 40 trials performed for each prescribed distance (Fig. 3.2). Subjects were again given 800 ms to complete each trial. They completed this variability task twice -- once before the four conditions (PRE), and again after completing the four conditions (POST). However, we did not introduce the 66-percent distance or the POST testing until after the first four subjects had participated in the experiment.

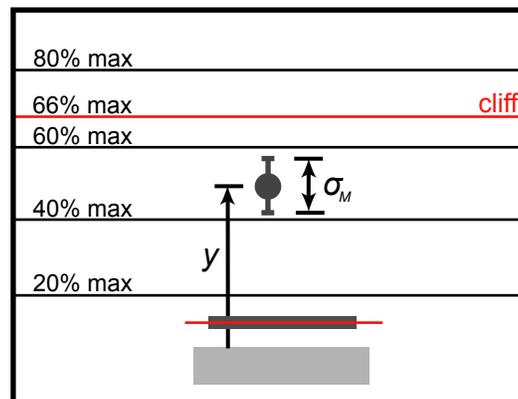


Figure 3.2. Variability testing. Visual feedback and variability, σ_M , associated with a mean movement endpoint, y , during variability testing (PRE and POST). Subjects moved a cursor to five discrete targets placed at percentages of their maximum movement distance, indicated by the thin horizontal black and red lines.

With a known movement distance y (mean endpoint when aiming for each discrete line), target width σ_M (variability of movement endpoints), and the corresponding movement time t , we can use an adapted relation of Fitts' Law (Faisal and Wolpert 2009) to estimate two subject-specific parameters c and d :

$$\sigma_M(y) = y 2^{\left(1 - \frac{t(y)-c}{d}\right)} \quad (3.1)$$

With this approach, we are able to estimate an individual's movement variability as a function of distance, where the movement time is fit as a linear function of movement distance, $t(y) = ay + b$, from the discrete line endpoint data. The only parameters needed as inputs to the SDT model were the four parameters a, b, c , and d , which we averaged from the PRE and POST tasks.

Data acquisition

In the ARM task, optical encoders sampled the position of the robot handle at 200 Hz. In the WB task, the forceplate recorded three-dimensional forces (F_x, F_y, F_z) and moments (M_x, M_y, M_z) about its center at 200 Hz. Center of pressure (COP) was calculated as $[COP_x \ COP_y] = [M_x \ M_y]/F_z$, where x and y refer to mediolateral and anteroposterior axes, respectively.

Risk-sensitivity

We quantified risk-sensitivity by comparing subjects' actual movement endpoints with endpoints predicted by a risk-neutral model of movement planning. We extended a model based on principles of statistical decision theory (SDT) (Trommershäuser et al. 2003) to calculate the risk-neutral movement endpoint for each subject in all four conditions. The model-predicted endpoint is dependent on a subject's sensorimotor variability (determined from our variability test) and the reward/penalty structure of the task.

In this model, a subject's expected gain function $\Gamma(S)$ for a chosen movement strategy S is a product of the probability of hitting a region R_i given that endpoint and the gain G_i associated with the region. In our experiment, the two regions of interest are the safe region R_{safe} (linear gain G_{safe} ranging from 0 to 100 points) and the cliff region R_{cliff} (gain G_{cliff} of 0 or -500 points). The expected gain as a function of movement distance is:

$$\Gamma(y) = \begin{cases} G_{\text{safe}}P(y'|y) & \text{if } y' \leq y_{\text{cliff}} \\ G_{\text{cliff}}P(y'|y) & \text{if } y' > y_{\text{cliff}} \end{cases} \quad (3.2)$$

We compute the probabilities $P(y'|y)$ by assuming that the actual movement endpoints, y' , are distributed around a planned endpoint, y , according to a Gaussian distribution and integrating over the entire landscape ($R_{\text{safe}} + R_{\text{cliff}}$).

$$p(y'|y) = \frac{1}{2\pi\sigma^2} \exp \{[-(y' - y)^2]/2\sigma^2\} \quad (3.3a)$$

$$P(y'|y) = \int_{R_{\text{safe}}+R_{\text{cliff}}} p(y'|y) dy' \quad (3.3b)$$

The total variance σ^2 is a combination of the noise added to the cursor and the subject's sensorimotor variability:

$$\sigma^2 = \sigma_N^2 + [\sigma_M(y)]^2 \quad (3.4)$$

With a subject's sensorimotor variability as a function of movement distance, this model computes the risk-neutral movement endpoint, or the endpoint that would maximize the expected number of points for a given condition in our cliff paradigm. This endpoint is further from the cliff edge under conditions of increased risk, introduced with increased penalty and/or variability, as illustrated in Figure 3.3.

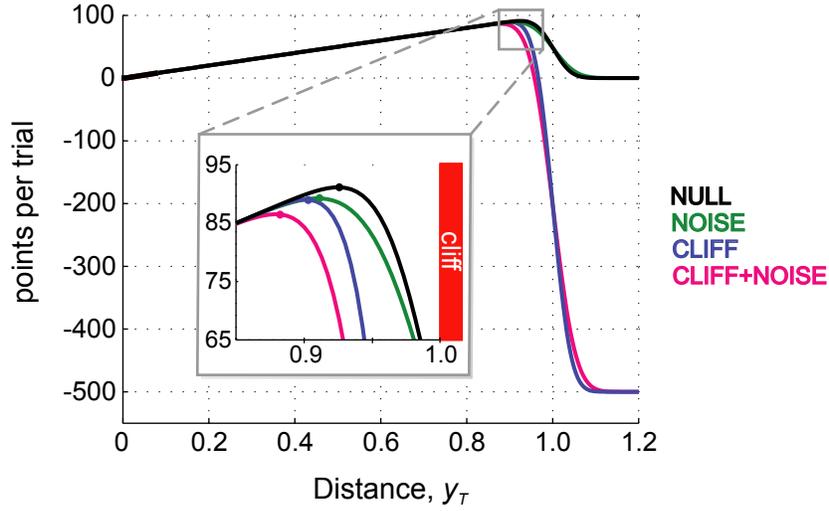


Figure 3.3. Risk-neutral movement planner. Sample model-predicted movement endpoints and expected gain landscape during the four conditions. The risk-neutral movement endpoint, y_T^{MEG} , maximizes the expected number of points per trial and is denoted by a dot on each condition's gain landscape. This endpoint recedes farther from the cliff edge in conditions of increased risk: greater penalty (500-point cliff penalty) and/or variability ($\sigma_N = 0.3\text{cm}$).

Risk-sensitivity is calculated from the ratio between a subject's mean endpoint, y_F , and his model-predicted endpoint, y_F^{MEG} , for each risk condition:

$$\text{risk-sensitivity (\%)} = 100 \left(\frac{y_F}{y_F^{MEG}} - 1 \right) \quad (3.5)$$

Thus, a risk-sensitivity of 0% indicates perfect agreement between the model prediction and the subject behavior (risk-neutral). A positive risk-sensitivity indicates that a subject moved farther than the model predicted (risk-seeking), and a negative value indicates that a subject did not move as far as the model predicted (risk-averse).

In this experiment, we can not only classify an individual as risk-sensitive or risk-neutral by his movement decisions in any given risk condition, but we can also compare movement across the different conditions to examine the consistency of risk-sensitivity. Comparing movement decisions across conditions may also allow us to determine whether risk-sensitive behavior could be explained by subject-specific distortions in the utility or probability weightings relevant to the virtual cliff paradigm.

We performed three separate analyses on all 20 subjects to investigate risk-sensitivity in each task and the transfer of risk-sensitivity between tasks. We repeated these analyses separately for the eight subjects who completed the conditions in a random order. First, we quantified the direction and degree of risk-sensitivity at the *group level* for each condition and movement task. From this analysis we could determine whether subjects exhibited consistent direction and degree of risk-sensitivity in each movement task. If risk-sensitivity was consistent across conditions, we can draw meaningful conclusions about subjects' overall risk-sensitivity for each movement. Importantly, this analysis would not detect transfer of risk attitudes if individual subjects were idiosyncratic in their risk-sensitivity, but maintained this risk-sensitivity across tasks.

To allow for different risk-sensitivities across subjects, yet still examine consistency across tasks we turned to a second analysis. Using the same risk-sensitivity data, we performed a *subject-level* analysis to determine whether the direction of risk-sensitivity was consistent between movements. If a subject was

risk-seeking in the arm-reaching movement, was he similarly risk-seeking in the whole-body movement? This involved paired comparisons between risk-sensitivity measures in each movement for each condition and was verified with a regression analysis at the group and subject levels.

Thirdly, to determine possible mechanisms underlying any observed risk-sensitivity, we fit subject-specific risk-sensitivity parameters and compared these parameters between movements. We adjusted our model to incorporate principles of cumulative prospect theory (CPT) introduced by Tversky and Kahneman (1992). In CPT, risk-sensitivity can be explained by either a distortion in the (1) utility function or (2) probability weighting function. This leads to an adjusted expected gain function $\Gamma'(y)$ that includes a utility and probability weighting functions $w(P)$, similar to that described by Wu et al. (2009).

$$\Gamma'(y) = \begin{cases} G_i^\alpha w(P), & \text{if } G_i \geq 0 \\ -(-G_i)^\beta w(P), & \text{if } G_i < 0 \end{cases} \quad (3.6a)$$

$$w(P) = \exp[-(-\ln(P(R_i|y)))^\gamma] \quad (3.6b)$$

In our experiment, distorted utility means inappropriately valuing the point rewards and penalties represented by coefficients α and β , respectively. An appropriate utility weighting then corresponds to $\alpha=\beta=1.0$. Given that many subjects demonstrated a risk-seeking behavior in the movement tasks, we would expect most subjects to overvalue rewards ($\alpha>1.0$) and undervalue penalties ($\beta<1.0$), which would likely result in moving closer to the cliff. An appropriate probability

weighting corresponds to $\gamma=1.0$, while $\gamma>1.0$ would represent the overweighting of large probabilities and the underweighting of small probabilities, thus manifesting risk-seeking behavior. We fit values of α , β , and γ for each of our subjects to determine whether distorted weighting of utility or probability could explain any observed risk-sensitivity. Specifically, we used the *fminsearch* function in MATLAB to find the weighting values that minimized the mean squared error between a subject's actual endpoints and the model predictions in all conditions. This function calculates the local minimum of an unconstrained multivariate function around an initial estimate ($\alpha=1.0$, $\beta=1.0$, $\gamma=1.0$).

Statistics

We performed a three-way repeated-measures analysis of variance (ANOVA) to determine whether there were effects of risk condition (including penalty and variability) or task on movement endpoints. We used independent t-tests to compare risk-sensitivity measures to 0% (*direction* of risk-sensitivity), and we used paired t-tests to compare risk-sensitivity measures between the ARM and WB tasks (*degree* of risk-sensitivity). In the latter case, we adjusted for multiple comparisons across the four risk conditions. For the group-level least-squares regression analysis, we verified statistical evidence for a linear relationship between ARM and WB risk-sensitivity with an F-test. We used an independent t-test to compare individual subjects' regression slopes to unity. We used paired t-tests for subject-specific comparisons between tasks, conditions, and CPT parameters. To adjust for

multiple comparisons across risk conditions, we used the Bonferroni correction, with the significance level set to 1.25%. For all other statistical tests, the significance level was set to 5%.

3.4 Results

Overview

We found that most subjects' endpoints followed the general trends predicted by a subject-specific model and risk-neutral movement planner. In both ARM and WB tasks, subjects avoided the cliff more with increasing point penalties and increasing noise. Overall, the *direction* of risk-sensitivity was consistent between the ARM and WB tasks, but the *degree* of risk-sensitivity did not transfer between these two movement types. These results hold when the order of conditions is randomized.

Movement trends

The mean distance from the starting position to the cliff edge was 15.4 ± 3.2 cm for the ARM task and 5.9 ± 1.4 cm for the WB task. We examined the last 100 trials of each condition. Movement endpoints for a representative subject (S8) performing the ARM and WB cliff tasks are shown in Figure 3.4A, with all endpoints normalized to that subject's cliff distance. We denote a movement

endpoint as y_T when referring to a distance traveled toward the cliff and as y_F when referring to a distance from the cliff ($y_F > 0$ corresponds to movements on the safe side of the cliff). The distribution of endpoints was approximately Gaussian for all subjects. On average, during these last 100 trials, subjects moved past the cliff edge the following number of times: in ARM, 8.5 ± 5.9 (NULL), 1.8 ± 2.5 (NOISE), 2.9 ± 2.7 (CLIFF), and 0.8 ± 1.2 (CLIFF+NOISE); in WB, 17.2 ± 7.6 (NULL), 8.0 ± 5.8 (NOISE), 6.1 ± 4.8 (CLIFF), and 2.6 ± 2.4 (CLIFF+NOISE).

Increasing penalty and variability significantly affected movement endpoints in both the ARM and WB tasks. Figure 3.4B illustrates that on average subjects follow the general trends predicted by the risk-neutral movement planner, and conditions of increased penalty and variability result in movement endpoints that are further from the cliff edge. On average, however, subjects move closer to the cliff edge than predicted by the risk-neutral model. This is particularly evident in the WB task.

We performed a three-way repeated-measures ANOVA on movement endpoint data to examine the effects of risk condition and movement task. The levels were penalty (0 or -500 points), variability (no added Gaussian noise and added Gaussian noise), and movement task (ARM and WB). We found independent effects of penalty, variability, and task ($p < 0.0001$), as well as a task*penalty interaction effect ($p < 0.002$). Thus, the high cliff penalty prompted a greater change in movement endpoints for the WB task than for the ARM task. A subsequent two-way rmANOVA of the risk condition at each level of movement task reveals

independent effects of both penalty and variability for ARM and for WB (Fig. 3.4C), indicating that adding the high cliff penalty and adding cursor noise significantly affected the endpoint for both movement tasks (p 's < 0.005).

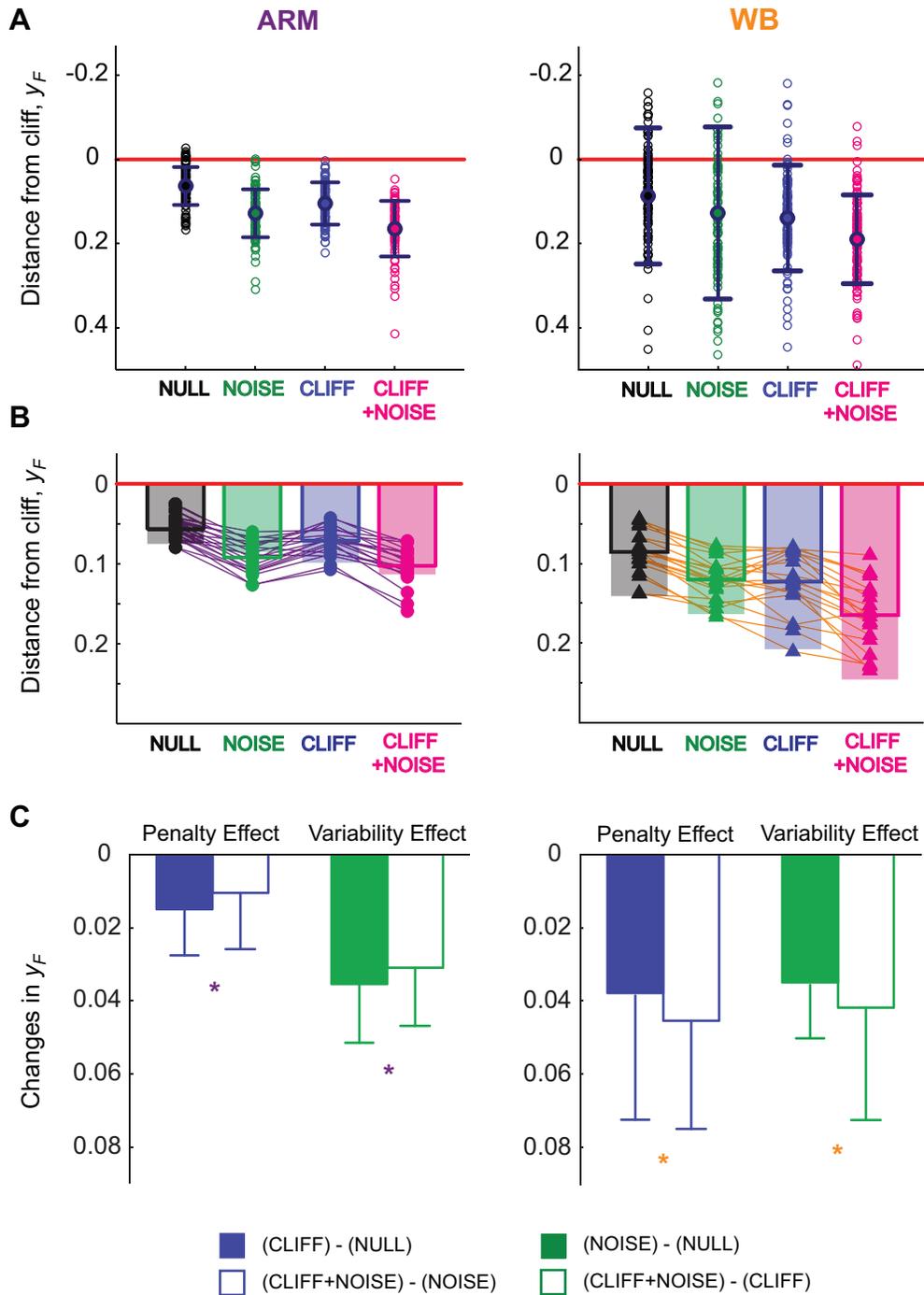


Figure 3.4. Movement trends. (A) Movement endpoints, including mean and standard deviation, for S8 during the four conditions for ARM (left) and WB (right). Endpoints are expressed as distance from the cliff, y_F , and are normalized by the subject's cliff distance. The cliff edge is shown as a solid red line. (B) Mean movement endpoints normalized by cliff distance for all subjects during the four conditions for ARM (left) and WB (right). Mean subject endpoints for each condition are denoted by the outlined bars, while mean endpoints predicted by the risk-

neutral model for each condition are denoted by the filled bars. **(C)** Independent effects of penalty and variability on movement distance for ARM (left) and WB (right). Effect of penalty is determined by subtracting mean endpoints of NULL from CLIFF (blue-filled bar) as well as NOISE from CLIFF+NOISE (blue-outlined bar). Effect of variability determined by subtracting mean endpoints of NULL from NOISE (green-filled bar) as well as CLIFF from CLIFF+NOISE (green-outlined bar). Asterisks (*) indicate significant differences from zero ($p < 0.05$).

Risk-sensitivity

Mean risk-sensitivity values, calculated from (3.5), are shown in Figure 3.5A for each subject, condition, and task. Group mean values are plotted in Figure 3.5B.

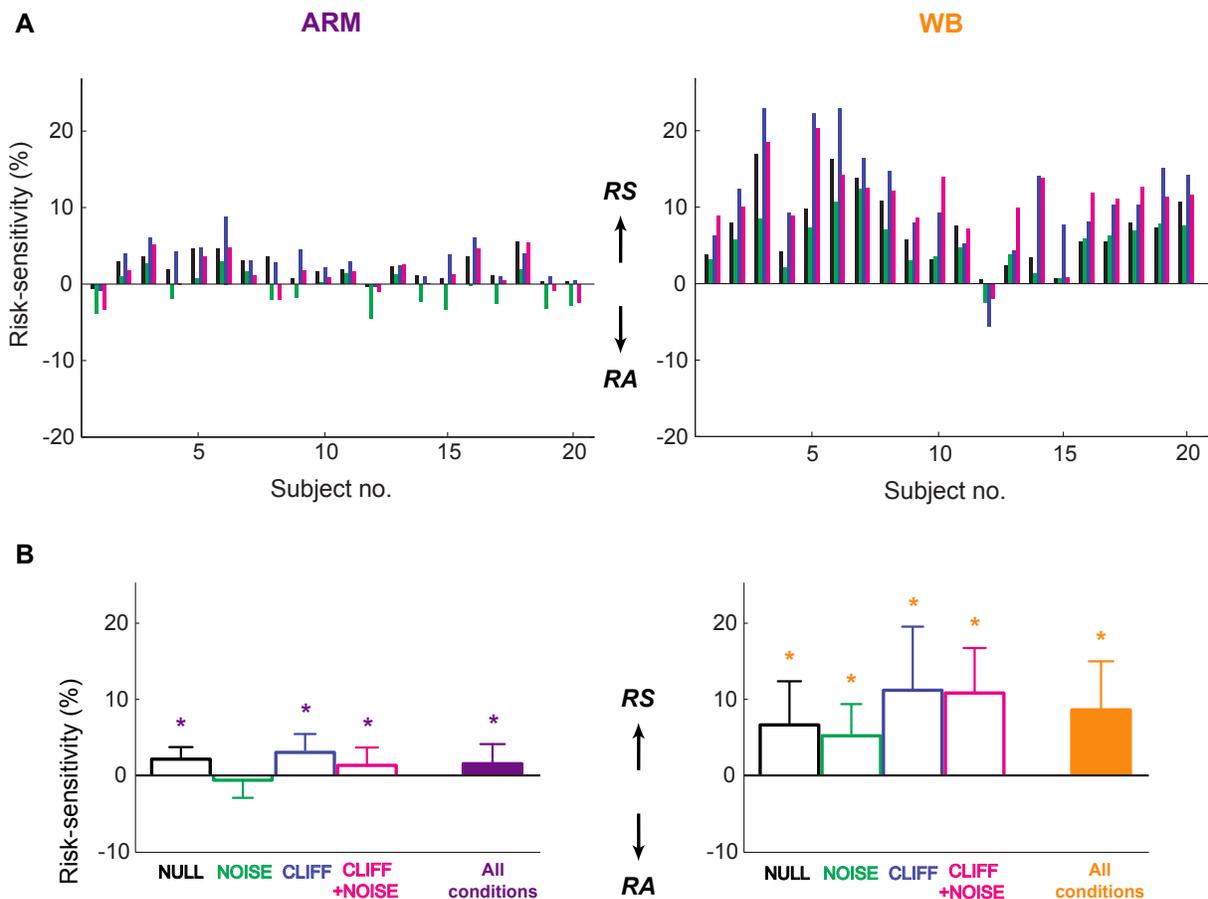


Figure 3.5. Risk-sensitivity. (A) Mean risk-sensitivity values for individual subjects in each of the four conditions for ARM (left) and WB (right). A value less than 0% indicates that a subject did not move as close to the cliff as predicted (risk-averse, RA), whereas a value greater than 0% indicates that a subject moved closer to the cliff than predicted (risk-seeking, RS). (B) Mean risk-sensitivity across subjects in each condition and across all conditions. Asterisks (*) indicate significant differences from 0%.

Independent t-tests show no significant difference between subjects' mean risk-sensitivity and 0% for the NOISE condition in the ARM task, whereas risk-sensitivity was greater than 0% in all other conditions in ARM and WB ($p < 0.05$). This is indicative of consistent risk-seeking behavior in both movement tasks. In the WB task, only one subject (S12) had a mean risk-sensitivity less than 0% in any condition (NOISE, CLIFF, CLIFF+NOISE). The same subject also had a mean risk-sensitivity less than 0% in all four ARM conditions, indicating relatively consistent risk-averse behavior for this subject. Only one subject (S1) demonstrated idiosyncratic risk preferences between movements in all conditions, with risk-averse behavior in ARM and risk-seeking behavior in WB. A paired t-test showed that risk-sensitivity values were significantly further from 0% in the WB task than in the ARM task for all four conditions (p 's < 0.002). Overall, subjects moved closer to the cliff in the WB task than the model predicted, and the discrepancy between actual endpoints and model-predicted endpoints is larger in the WB task than in the ARM task.

We turn to our second analysis to determine the consistency of risk-sensitivity across tasks for each subject. Figure 3.6 further illustrates the consistent *direction* of risk-sensitivity between movement tasks and the disparate *degree* of risk-sensitivity between movement tasks. Of the 80 available data points quantifying average risk-sensitivity (20 subjects x 4 conditions), 62 points were either risk-seeking in both ARM and WB or risk-averse in ARM and WB. This means that the direction of risk-sensitivity transferred across the two movements in

77.5% of all cases. A least-squares linear regression of group WB risk-sensitivity against ARM risk-sensitivity resulted in a regression slope of 7.2 ($R^2 = 0.30$, $F = 22.3$, $p < 0.0001$), confirming that subjects were more risk-seeking in WB. This finding held when we performed the same linear regression at the subject level; across subjects, the slopes of the regression line between conditions were significantly greater than unity ($p < 0.001$), with a mean (\pm SD) slope of 6.1 (± 4.1) and a mean (\pm SD) R^2 of 0.36 (0.29).

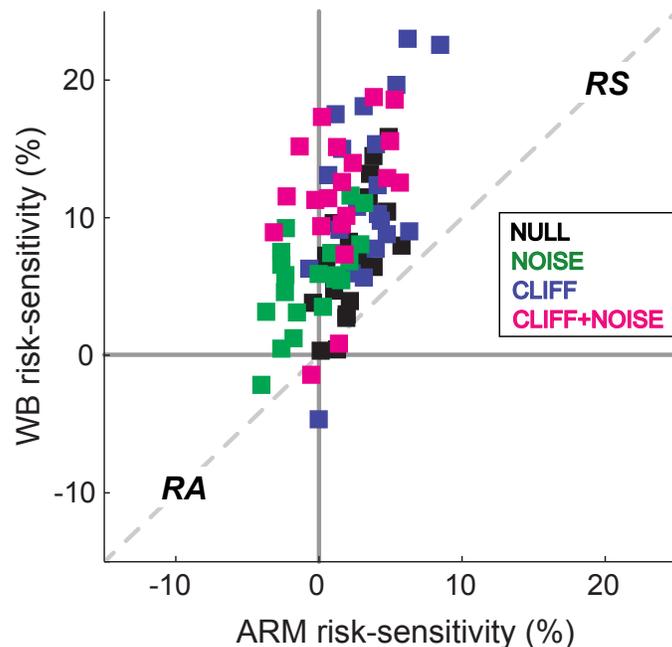


Figure 3.6. Degree of risk-sensitivity. Risk-sensitivity for individual subjects in each condition, comparing ARM and WB. Data points that fall in the upper right quadrant correspond to risk-seeking behavior (RS). Data points that fall in the lower left quadrant correspond to risk-averse behavior (RA). Unity is shown as a dashed black line. Least-squares linear regression for this comparison yields a slope of 7.2, confirming that the degree of risk-sensitivity is greater in the WB task (i.e. more risk-seeking in WB than ARM).

Our final analysis of risk-sensitivity sought to establish whether these deviations from 0% risk-sensitivity could be a manifestation of distorted utility or distorted probability weighting. We fit the weighting parameters α , β , and γ from (6a) and (b) for each subject. Altering the utility and probability weighting functions shifts subjects' mean risk-sensitivity closer to 0% for both the ARM and WB movements, indicating that distortion of the α , β , or γ values could explain subject behavior during our experiment. In the ARM movement, our mean fit values are $\alpha=1.13\pm 0.17$, $\beta=0.76\pm 0.31$ and $\gamma=1.13\pm 0.22$. In the WB movement, our mean fit values are $\alpha=1.42\pm 0.27$, $\beta=0.33\pm 0.37$, and $\gamma=1.22\pm 0.17$. Across subjects, the three fit weighting parameters are significantly different from 1.0 in both movement tasks. These parameter fits corroborate our experimental observations of consistent risk-sensitivity across movements. Consistent with risk-seeking behavior, most subjects (17 out of 20) overvalue the point rewards ($\alpha > 1.0$), undervalue penalties ($\beta < 1.0$), or overestimate their movement accuracy ($\gamma > 1.0$) in both movements. Only one subject (S12) has parameters that align with risk-averse behavior in both movements, and two subjects (S1 and S20) have parameters that show idiosyncratic risk-sensitivity (risk-averse in ARM, risk-seeking in WB). For the two utility parameters α and β , there are significant differences between the ARM and WB tasks (α : $p=0.0002$; β : $p=0.0001$), indicating that distortions are larger in the WB movement. This also supports our behavioral findings of greater risk-seeking behavior in whole-body movements. There is not a significant difference in the variability parameter γ between ARM and WB ($p=0.087$).

Effects of learning

Subjects did not appear to learn a movement strategy during the course of the experiment for either movement task. To determine whether subjects learned during the experiment, we examined both movement error and standard deviation of endpoints during each condition. For our purposes, movement error is equivalent to y_F , the distance between a subject's endpoint and the cliff edge. Most subjects do not exhibit a significant change in movement error during any given condition when comparing the first 10 trials and the last 10 trials (p 's >0.05). The only exceptions to this are S2 (NULL $p=0.024$), S3 (CLIFF+NOISE $p=0.008$), S11 (CLIFF $p=0.005$), and S13 (CLIFF+NOISE $p=0.002$) in the ARM task, as well as S6 (CLIFF $p=0.038$, CLIFF+NOISE $p=0.025$), S8 (CLIFF+NOISE $p=0.037$), and S16 (NOISE $p=0.039$) in the WB task. There was no significant change in the standard deviation of movement endpoints between the first 10 trials and the last 10 trials (p 's >0.05) in any condition and across all subjects.

Variability testing

One challenge in determining a risk-neutral movement endpoint is that movement variability changes as a function of time and distance. We had accounted for this changing variability in a separate experiment for each movement task, which allowed us to estimate subject-specific variability as a function of distance. For example, each subject's *measured* sensorimotor variability at the cliff distance, $\sigma_M(y_{\text{cliff}})$, and the *estimated* variability at the cliff distance, $\sigma_{0.66}$, is provided in

Table 1. We determined these variability functions from the averages of each subject's PRE and POST variability measurements. However, POST variability data was not available for subjects S1-S4, since we did not instate POST testing until after these four subjects had completed testing. Furthermore, we did not use the PRE data for S12 WB or the POST data for S15 WB because these subjects did not follow Fitts' Law in these cases. Specifically, variability decreased with movement distance in these two instances. Since this behavior was not consistent between the PRE and POST tests for these subjects, we attributed the results to external factors such as distracted attention or fatigue and questioned their validity as a true representation of the subject's sensorimotor variability.

The mean (\pm SD) values of the measured variability when moving to the 66% target line are 0.53 (0.15) cm in ARM and 0.53 (0.14) cm in WB. Note that this average variability only includes S5-S20, since the 66% target line was not incorporated for the first four subjects. With the exception of S3, S4, S5, S6, and S17 in ARM, all estimated variabilities at the cliff distance were equal to or slightly less than the measured values. This indicates that the estimated functions $\sigma_M(y)$ were adequate representations of subject-specific sensorimotor variability. Estimating a lower variability than the measured would produce model predictions that are slightly closer to the cliff. This means that the difference between actual endpoints and risk-neutral predicted endpoints would be *smaller* for subjects who move beyond the model predictions and *larger* for subjects who do not move as close to the model predictions. From (3.5), underestimating a subject's sensorimotor variability

would thus result in decreased risk-sensitivity values across conditions (portraying a risk-seeking individual as less risk-seeking, a risk-averse individual as more risk-averse, and a risk-neutral individual as risk-averse).

Table 3.1. Subject variability and probability distortion.

Subject	ARM		WB	
	$\sigma_M(y_{\text{cliff}})$ (cm)	$\sigma_{0.66}$ (cm)	$\sigma_M(y_{\text{cliff}})$ (cm)	$\sigma_{0.66}$ (cm)
S1	0.39	(0.42) [†]	0.36	(0.42) [†]
S2	0.56	(0.82) [†]	0.60	(0.60) [†]
S3	0.84	(0.82) [†]	0.51	(0.66) [†]
S4	0.50	(0.44) [†]	0.48	(0.48) [†]
S5	0.50	0.48	0.44	0.66
S6	0.55	0.53	0.57	0.60
S7	0.62	0.64	0.60	0.67
S8	0.46	0.46	0.68	0.69
S9	0.58	0.63	0.31	0.57
S10	0.67	0.73	0.70	0.73
S11	0.76	0.88	0.41	0.67
S12	0.61	0.61	0.32	0.52 [‡]
S13	0.46	0.54	0.22	0.25
S14	0.30	0.33	0.38	0.47
S15	0.42	0.42	0.36	0.38 [†]
S16	0.59	0.62	0.33	0.33
S17	0.47	0.46	0.39	0.51
S18	0.41	0.44	0.34	0.38
S19	0.43	0.43	0.45	0.48
S20	0.26	0.28	0.59	0.62

Table 3.1. Estimated sensorimotor variability at the cliff distance, $\sigma_M(y_{\text{cliff}})$, and measured variability at the cliff distance (averaged from PRE and POST variability testing), $\sigma_{0.66}$, for each subject and movement task. Also includes the ratio of external noise to each subject’s variability at the cliff distance to illustrate the extent of added uncertainty in the NOISE and CLIFF+NOISE conditions. Since we did not introduce the 66% target line or POST variability testing until after the first four subjects, $\sigma_{0.66}$ values given for S1-S4 are interpolated from variability at the 60% and 80% target lines during PRE testing and are shown in parentheses.

[†] From PRE variability data only

[‡] From POST variability data only

Generally, subjects tended to move slightly past the target line, overshooting by an average of 1.1% in the ARM movement and 4.8% in the WB movement. Interestingly, subjects were able to move nearly as precisely in the WB movement as in the ARM movement during this variability test. For example, the measured endpoint variability at the 0.66% target line, $\sigma_{0.66}$, is comparable between the two tasks (see Table 1); a paired t-test reveals that there is no significant difference in $\sigma_{0.66}$ between ARM and WB ($p=0.94$, S5-S20). This is also true for the 40-, 60-, and 80% target lines, with no significant differences between ARM and WB measured endpoint variability (p 's >0.3 , S1-S20). Only for the 20% line was subject endpoint variability lower in the ARM task than in the WB task ($p<0.001$).

Model adjustments

It is certainly possible our subject-specific variability functions did not accurately capture the subject's true endpoint variability and led to different estimates of risk-neutral movement behavior and thus different values of subject risk-sensitivity. We examined alternative variability functions as inputs to the SDT model and the resulting effects on risk-sensitivity. Considered alternatives included (1) parameters from PRE testing, (2) parameters from POST testing, (3) a constant sensorimotor variability from PRE and POST testing, and (4) a constant sensorimotor variability from each cliff condition. However, these adjustments did not yield any consistent decrease in risk-sensitivity for our subjects. Most often, these model adjustments would precipitate values that deviated even further from

0%. Overall, we feel confident that with our available data, we have presented a “best-case” scenario in comparing subject endpoints to risk-neutral model predictions.

3.5 Conclusions and Discussion

This is the first study to assess risk-sensitivity in goal-directed whole-body movements and to compare risk-sensitivity across two dissimilar movements. We have shown that increasing risk in the form of point penalties and/or variability does affect movement endpoints in both arm-reaching and whole-body movements, and we present evidence of risk-sensitivity in whole-body movements. Overall, our findings demonstrate that subjects were generally risk-seeking in both movements. However, the *degree* of risk-sensitivity did not transfer between the two movements. In this section, we discuss each movement in turn, compare behavior in the two movements, and provide possible explanations for the differences between them.

In the arm-reaching task, movement endpoints are slightly closer to the cliff edge than predicted by the SDT model in three of the four risk environments, indicating that subjects are risk-seeking in these movements. This does not support previous findings of risk-neutral planning behavior in the hand/arm system under symmetric expected gain landscapes (Trommershäuser et al. 2003, 2008). Indeed, predicted endpoints more closely matched subject endpoints when we incorporated distortions in utility and probability weightings into the model that were distinctive

of risk-seeking behavior. However, Wu et al. (2006) found that subjects performed suboptimally when pointing in an asymmetric expected gain landscape. In this case, the authors conjecture that subjects are not able to maximize expected gain in an asymmetric environment due to the increased complexity of the movement planning task. The expected gain landscape presented in our study is different than that of Wu et al. but is still inherently asymmetric, supporting their findings of suboptimal behavior.

In the whole-body leaning movement, increasing risk also significantly affected subjects' movement endpoints. A number of previous studies have shown an effect of implicit postural threat (i.e. an elevated support surface) on the control of center of pressure (Adkin et al. 2000, 2002; Brown et al. 2006; Carpenter et al. 2001, 2006; Davis et al. 2009), but this is the first study to quantify the influence of explicit risk on goal-directed center of pressure movements in a decision-making framework. Movement endpoints in this task are decidedly closer to the cliff than predicted by the model, indicating that subjects are not risk-neutral in whole-body leaning movements. Again, risk-seeking distortions in utility and probability generated model-predicted endpoints that more closely matched subjects' endpoints, further attesting to a general risk-seeking attitude during this movement. This evidence of risk-seeking behavior is unexpected, particularly in light of previous findings demonstrating that increased postural threat leads to more cautious whole-body movement control (Adkin et al. 2002).

Despite the distinct biomechanical differences between these two types of movement, we find that subjects adapt similar directionality in their risk-sensitivity. Recent studies have investigated whether risk-sensitivity transfers across other decision-making tasks and domains at the behavioral and neurobiological levels. Wu et al. (2009) observed dissimilar direction of risk-sensitivity in the same subjects in different decision making domains: a financial task and a movement task. However, when comparing tasks involving either food or financial rewards, Levy and Glimcher (2011) found that directionality of risk-sensitivity is correlated. Their corresponding neuroimaging results suggested that there may be overlapping neural substrates for risk-sensitivity across task domains. Likewise, our results suggest that there may be overlapping substrates for risk-sensitivity in movement control, but individuals can maintain different degrees of risk-sensitivity.

Our other main finding is that while the direction of risk-sensitivity was similar between movements, we did not see a similar *degree* of risk-sensitivity. Subjects were more risk-sensitive in the whole-body movement compared with arm-reaching. Thus, an individual's movement decision making in one movement does not fully predict their performance in another. Subjects tended to adopt a risk-seeking strategy during arm-reaching, but they were markedly more risk-seeking in the whole-body movement. Why doesn't the degree of risk-sensitivity directly transfer from one movement to another? Our model indicates that subjects could possess distorted utility and probability weighting functions and that these

distortions differed between movements. In our experiment, such distortions could have arisen from: (i) an inaccurate estimation of sensorimotor variability, (ii) a subject not responding appropriately to the explicit point-based rewards/penalties, or (iii) our model of risk-neutral movement planning overlooks an underlying cost of motor control and is unable to predict subject behavior. We next address each of these possibilities in turn.

Risk-seeking behavior could result from an inappropriate estimation of task-related sensorimotor variability, by either the subject or the experimenter. A subject may internalize an estimation of their variability that causes overweighting large probabilities and underweighting small probabilities (distortion in probability). This means that subjects believe themselves to have a smaller endpoint variability than they actually do, which would most likely influence them to move closer to the cliff edge than predicted. Wu et al. (2009) observed a similar distortion pattern during a rapid pointing motor task, when the probability in question was simply subjects' own implicit sensorimotor uncertainty. We believe that inaccurate variability estimation is a manifestation of unfamiliarity with the motor task. Although forward leaning movements are relatively common in everyday tasks (such as when reaching for a cup in a high cabinet), such movements tend to involve slow, small leaning distances. However, the rapid, "out-and-back," goal-directed center of pressure movements utilized in our experiment are difficult and are not often experienced on a daily basis. This could account for an inability to appropriately internalize one's sensorimotor variability within the duration of this experiment.

It is possible that our estimation of subjects' variability does not accurately reflect their true endpoint variability. Because our quantification of risk-sensitivity is dependent on this variability estimation, our results may be biased toward a consistent direction or degree of risk-sensitivity. We explored alternative measurements of variability to adjust our SDT model; however, these adjustments typically resulted in increased risk-sensitivity values (subjects were more RS). We feel that we have presented a best-case scenario with our variability test data to compare subject endpoints with risk-neutral model predictions.

Alternatively, risk-seeking behavior could stem from overweighting point rewards and underweighting point penalties associated with the cliff paradigm (distortion in utility). However, we find this unlikely for two reasons. First, the point structure was the same in both the arm-reaching and whole-body tasks, so there is no obvious reason why the same subject would value these points differently between tasks. Even if a distorted utility function does exist, this distortion should remain consistent between tasks, which is not what we observe. Secondly, if anything, leaning forward closer to the limits of stability while standing should lead to an overweighting of the point penalties and result in more risk-averse behavior compared with the arm-reaching task. Leaning forward inherently increases the chance of a fall, thereby adding an implicit penalty over and above the explicit point penalties presented to the subject (Adkin et al. 2002). Individuals do indeed alter postural control strategies under greater implicit penalty, such as that imposed by standing on an elevated platform. These altered strategies – including

decreased maximum reach, slight backward leaning, or reduced variability of postural sway – arguably align with risk-averse behavior and have been associated with both voluntary (Hauck et al. 2008) and involuntary (Davis et al. 2009; Brown et al. 2007) leaning.

Given the dissimilar natures of arm-reaching and whole-body movements, it is certainly possible that these movements incorporate different control strategies or motor costs that are not included in our model. One potential candidate is an effort cost of muscle activation. In the arm-reaching movement, effort cost increases with movement distance. Adding an effort cost would lead to shorter movements, similar to the effect of increased variability. However, the relationship between center of pressure movement and effort in this rapid out-and-back task has yet to be determined. In the WB task, the biomechanical properties of the foot/ankle are very different from the arm/hand and may contribute significantly to effort quantification or variability in the WB task. For instance, it could be more desirable to move the COP closer to the balls of the feet because of more comfortable or familiar activation strategies in the foot/ankle, or due to some heightened control capabilities afforded by the COP's proximity to the toes. Theoretically, this could lead to a distortion in the underlying utility function, which would be different in the whole-body task than in arm-reaching. If moving greater distances required less effort or offered greater control, this would be manifested in the subject's behavior as an overvaluation of reward and undervaluation of penalty. Furthermore, subjects may be knowingly choosing a “satisficing” strategy over an optimal strategy (Simon

1956), and since the costs and familiarity of the whole-body movement are conceivably different than an arm-reach, this may also explain the larger deviations from model predictions seen in the WB task.

We used a CPT analysis to fit possible subject-specific distortions in the weighting of reward, penalty, and variability. The resulting trends in parameters support our findings of risk-seeking behavior in both movements and a greater degree of risk-seeking behavior in the whole-body task. Furthermore, the CPT analysis indicates that this risk-seeking behavior is not solely a result of variability distortions (and thus potential misestimates of variability by the subject). Rather, the CPT fits point toward a distortion in the subjective value of the gain landscape. Although the ability to verify the accuracy of this fitting procedure is always a concern, we hope to further address this in future studies.

In this experiment, we characterize movement in the arm-reaching and whole-body tasks with hand endpoint and center of pressure (COP) endpoint, respectively. The COP is related to, but not equivalent to, the body's center of mass (COM). During upright postural adjustments, COP is the controlling variable, while COM is the controlled variable (Winter et al. 1998). The COP overshoots the vertical projection of the COM to keep the COM within the base of support, and the difference COP-COM is highly correlated with the negative acceleration of the COM. The difference between COP and COM is evident at the endpoint of a forward voluntary lean (Mancini et al. 2008) and becomes even greater during rapid out-and-back movements (Murnaghan et al. 2009), as is required in our study. Thus, we

are comparing incongruous measures between the two movement tasks (controlled variable in ARM and controlling variable in WB), and the COP (controlling variable in WB) is overshooting the COM (controlled variable in WB) at the movement endpoint. Initially, this may appear to explain the differences in degree of risk-seeking behavior observed between the ARM and WB tasks. However, we argue that using COP feedback in the WB task rather than COM does not change our interpretation of risk-sensitivity. In both movement tasks, we provide subjects with explicit visual feedback of the variable they are being asked to control (hand position in ARM, COP position in WB). The fact that COM will always lag behind COP at the movement endpoint does not ensure that subjects will move their COP beyond the target provided in the WB task. Rather, they likely control their movements such that the COP lands on or near the target, and the COM will be influenced by these dynamics accordingly. We see no reason why subjects would control their COM when specifically asked to control their COP and given the necessary feedback to do so. Indeed, a previous study from our lab confirms that subjects can control their COP in a goal-directed manner when instructed to do so, even when the target changes location mid-movement (Huang and Ahmed 2011). Even if they controlled their COM at the onset of the present experiment, one would expect them to adjust any unexpected endpoint behavior based on the scoring feedback provided. However, we generally do not observe an effect of learning or altered movement strategies throughout the duration of a trial set. Furthermore, all subjects were able to move to various distances on the “safe” side of the cliff, as

evidenced by performance during the PRE and POST variability testing. Nevertheless, many subjects would express verbal disappointment if they did not earn a score in the 80's or 90's, though they might repeatedly move past the edge of the cliff. We therefore do not attribute greater risk-seeking behavior in WB to an impaired ability to control COP over COM, but instead consider risk-sensitive behavior as a manifestation of the aforementioned possibilities (inappropriate variability estimation, inappropriate reward/penalty weighting, or an unaccounted cost).

It should also be noted that we did not scale the Gaussian cursor noise to the cliff penalty, so our various manipulations of risk (increasing variability and/or penalty) may not be equivalent. This could explain why we observe greater risk-sensitivity under conditions of increased penalty (CLIFF over NULL and CLIFF+NOISE over NOISE) than under conditions of increased variability (NOISE over NULL and CLIFF+NOISE over CLIFF). We expect that adding cursor noise with an even larger amount of standard deviation would still cause risk-seeking behavior in both movement tasks. This behavior does not align with that observed by Nagengast et al. (2010), where subjects acted risk-averse in the presence of cursor noise during a goal-directed arm-reaching movement in the horizontal plane. Nonetheless, these findings highlight the potential sensitivity of results to experimental context and the importance of controlling for context and inter-individual differences in this and future studies.

Our findings have important implications for quantitative descriptions of decision making to generalize across movements and, ultimately, across decision-making contexts. Further research is required to determine whether and to what extent risk-sensitivity transfers across these contexts, the neural structures governing such mechanisms, and under what conditions we may observe transfer across decision-making domains.

CHAPTER 4

THE EFFECT OF POSTURAL THREAT ON MOVEMENT RISK-SENSITIVITY

4.1 Abstract

Recent work indicates that emotional states such as sadness, anger, and threat play a critical role in decision-making processes. Here we addressed the question of whether risk preferences are influenced by postural threat and whether this influence generalizes across motor tasks. We examined risk attitudes in the context of arm-reaching and whole-body leaning movements, expecting that increased postural threat would lead to proportionally similar changes in risk-sensitivity for each motor task. Healthy young adults were shown a series of two-alternative forced-choice lotteries, where they were asked to choose between a riskier lottery and a safer lottery on each trial. Our lotteries consisted of different monetary rewards and target sizes. Subjects performed each choice task at ground level and atop an elevated platform. To determine risk-sensitivity, we quantified the frequency with which a subject chose the riskier lottery and fit lottery responses to a choice model based on cumulative prospect theory. Subjects exhibited idiosyncratic changes in risk-sensitivity between motor tasks and between elevations. However, we found that overweighting of small probabilities increased with postural threat in the whole-body task, indicating a more cautious strategy is ascribed to the possibility of a fall. Subjects were also more risk-seeking in the whole-body movements than in arm-reaching at low elevation; this behavior does

not seem to derive from consistent distortions in utility or probability representations but may be explained by subjects' inaccurate estimation of their own motor variability. Overall, our findings suggest that implicit threat can modify risk attitudes in the motor domain.

4.2 Introduction

Recent work suggests that an individual's emotional state can dictate decision making. For instance, affective reactions to a stimulus, either positive or negative, can alter our subjective interpretations of perceived risks and benefits, thereby impacting our cognitive processes and choices (Finucane et al. 2000; Slovic 1987; Slovic et al. 2004, 2007; Loewenstein et al. 2001; Loewenstein and Lerner 2003). Such a connection between emotion and decision making highlights an intriguing yet underappreciated finding in whole-body movement control. Even when there is a minimal increase in postural threat, individuals significantly alter their movement strategies (Huang and Ahmed 2011, Manista and Ahmed 2012, Piencak-Siewert et al., 2014). Elevation, in particular, is a method of increasing postural threat that has a marked effect of on movement strategies in whole-body movement control. Indeed, when asked to walk or simply stand on an elevated platform, both young and old adults reduce the velocity and extent of their movements (Brown et al. 2006; Adkin et al. 2000, 2002, 2008; Carpenter et al. 1999, 2001, 2006; Davis et al. 2009; Lamarche et al. 2009). While changes in movement

control on elevated platforms cannot be explained by changes in biomechanical capacity, they can be explained by risk-sensitive changes in decision making. Increased postural threat, modulated by standing on an elevated platform, leads to increased measures of physiological arousal, which indicates greater levels of anxiety (Ashcroft et al. 1991; Brown et al. 2002, 2006). Framing whole-body movement in neuroeconomic terms suggests that changes in decision making can result from feelings of threat associated with standing on an elevated platform. If changes in movement control on elevated platforms result from the feelings of threat experienced while standing on the platform, then it is feasible that these emotions will influence risk-sensitive behavior in motor-based tasks as well.

Previously, we investigated risk-sensitivity in arm-reaching and whole-body movements using a continuous movement paradigm (O'Brien and Ahmed 2013). Subjects maneuvered a cursor as close to the edge of a virtual cliff as possible and received a point score based on their performance. We found that in both movement tasks, subjects moved closer to the cliff edge than predicted by a risk-neutral model of movement planning, suggesting risk-seeking behavior. We also saw greater risk-seeking behavior in the whole-body movement than in arm-reaching. However, the cause of such behavior was unclear. A follow-up study intimated that differences in risk-sensitivity between the two tasks emerged from the movements themselves rather than from the sitting and standing postures (O'Brien and Ahmed 2014). We proposed that risk-seeking behavior in movement might have resulted from (i) an inappropriate estimation of sensorimotor variability, (ii) a distorted weighting of

point rewards and penalties, or (iii) an underlying cost of motor control not accounted for in our model. In the present experiment, we specifically addressed (i) and (ii) by probing subjects' subjective valuation of probability and utility (reward) during a movement task.

The main objective of this study was to examine the influence of postural threat on risk preferences during movement decision making and to assess whether this influence generalizes across different motor tasks. Subjects were asked to choose between risky and safe lotteries in the context of two motor tasks: arm-reaching and whole-body leaning. They completed each task at ground level and atop an elevated platform. We expected that increasing postural threat in the form of elevation (low vs. high) would lead to increased risk-aversion, with proportionally similar changes for both motor tasks. That is, if an individual became more risk-averse in the arm-reaching task at high elevation, that person would be equally risk-averse in the whole-body task at high elevation. Findings of this study are pertinent to the analysis of the influence of emotional state on movement decisions under risk. Our results will help determine whether there are generalizable principles such that movement decision-making in various emotional states can be predicted and trained across motor tasks.

4.3 Materials and Methods

Ethics statement

All subjects provided written informed consent before participation. The experimental protocol (12-0458) was approved by the Institutional Review Board of the University of Colorado Boulder in accordance with federal regulations, university policies, and ethical standards regarding human subject research.

Subjects

Twenty right-handed, healthy subjects (13 females, 7 males; mean age, 23.1 ± 2.8 years) participated in this experiment, performing two motor lottery series in both the low-threat and high-threat conditions. Thirteen of these subjects were part of a broader study examining the influence of threat on non-motor and motor tasks (O'Brien and Ahmed 2014). All participants provided informed consent, and the experimental protocol was approved by the Institutional Review Board of the University of Colorado Boulder.

Experimental protocol

Subjects performed two motor choice tasks: one for seated arm-reaching (ARM) and another for standing whole-body leaning movements (WB). In each task, subjects were asked to choose between two lotteries, where each lottery has a different monetary reward and probability of winning that reward. Rather than

offering explicit probabilities for these lotteries (e.g. 50% chance of winning the reward), we gave subjects implicit probabilities in the form of rectangular targets with variable widths (e.g. such that a subject had a 50% chance of hitting the target in a given motor task), wherein hitting the target results in winning the reward.

Subjects underwent a testing session in both motor choice tasks under two threat conditions: low elevation and high elevation. In the low elevation condition (Low), subjects chose between risky lotteries at ground level, either sitting in a chair for the ARM task or standing at the edge of a forceplate for the WB task. In the high elevation condition (High), subjects sat in the same chair or stood on the same forceplate at the edge of an elevated platform, 0.8m off the ground. The height of this elevated platform is approximately the average height at which young adults perceived they would not be able to use a step down strategy to descend from an elevated surface (Brown and Frank 1997). When standing in either elevation condition, subjects were secured in a harness and fall protection system that could arrest a fall before the subjects' knees touched the platform. However, to maintain perceptions of postural threat in the presence of this added safety, there was enough slack to the harness to allow subjects to move without restraint, and they were not allowed to voluntarily explore the competence of the fall protection system.

Prior to testing at each elevation, subjects were given the opportunity to practice actual movements in a training session. In the ARM task, subjects used their dominant arm to grasp the handle of a robotic manipulandum (Interactive Motion Technologies Shoulder-Elbow Robot 2) and move a cursor from a starting

region to a target that was 12cm directly in front of them. In the WB task, subjects stood on a forceplate (AMTI Dual-Top AccuSway, which is 4.5cm in height) and used their center of pressure to move the cursor from a starting region to a target that was 6cm directly in front of them. Figure 4.1A and 4.1B illustrate the physical configuration for the ARM and WB tasks, respectively. The cursor was a yellow circle with a radius of 0.25cm and a red vertical line through it to mark the center. The target was a thin, white horizontal line traversing the computer screen and a small, white vertical line at its center. Subjects were instructed to make a quick out-and-back movement from the starting region to the target, trying to move as straight as possible to hit the center of the target with the center of the cursor. However, the horizontal position of the cursor was obscured from the time the cursor left the starting region until they crossed the target line. Visual feedback of the cursor's horizontal position at the target distance was shown after each trial, supplying information about their error relative to the center of the target. We encouraged subjects to hit the target within 750-850ms by providing feedback about their movement time after each trial. During this feedback, the target flashed green if they moved too quickly, grey if they moved too slowly, and yellow with an auditory tone if they hit the target within the given time window. Subjects performed 100 trials in both ARM and WB tasks. We explicitly told subjects to pay attention to their performance throughout training, noting how close their cursor was to the target center across trials. We explained that having some idea of their

accuracy would help them make decisions about relative target sizes during the choice-based testing session.

During testing, subjects performed the ARM and WB lottery tasks in a randomized order at each elevation, counterbalanced across the two tasks. They completed both choice tasks at low elevation before performing them high elevation (Fig. 4.1C). It has been previously shown that increasing elevation results in more pronounced changes to postural control variables than decreasing elevation (Adkin et al., 2000). In always presenting the Low elevation condition first, we intended to capitalize on these order effects to maximize potential changes in risk-sensitivity due to threat. Ideally, we would test and re-test as many conditions as possible to examine consistency of choices over the different conditions. However, due to the overall length of the experiment and to minimize mental fatigue, we had subjects repeat one of these tasks, which we still used to examine choice consistency. We selected the WB Low task as the condition to be repeated. Our final 15 subjects performed this repeated condition, which was included in the randomized conditions at Low elevation. Lotteries were displayed on a computer monitor in front of the subject. In the testing phase of the experiment, subjects simply chose between pairs of lotteries, with every choice completing a single trial. Subjects performed 72 choice trials for each motor task. Within each trial, lottery information was shown for 4 seconds; the lotteries then disappeared and subjects were given 2 seconds to select their preferred lottery.

After completing the training and choice tasks at both elevations, subjects participated in a realization of choices phase, where we randomly selected one trial from each task, and the subject “played” their choice on that trial for real money. Playing a choice was similar to the training tasks; however, rather than showing a thin target line, subjects saw the specific target and monetary reward they chose on the selected trial. Subjects rapidly moved the same cursor to the chosen target; if the cursor hit the target, the subject won the reward. Since movement control is inherently variable, there was always a probability that a subject would miss the target (thereby receiving no reward) in these motor tasks. Subjects were aware in advance that a random selection of trials would be played to encourage them make decisions based on what they would do in a real-life scenario.

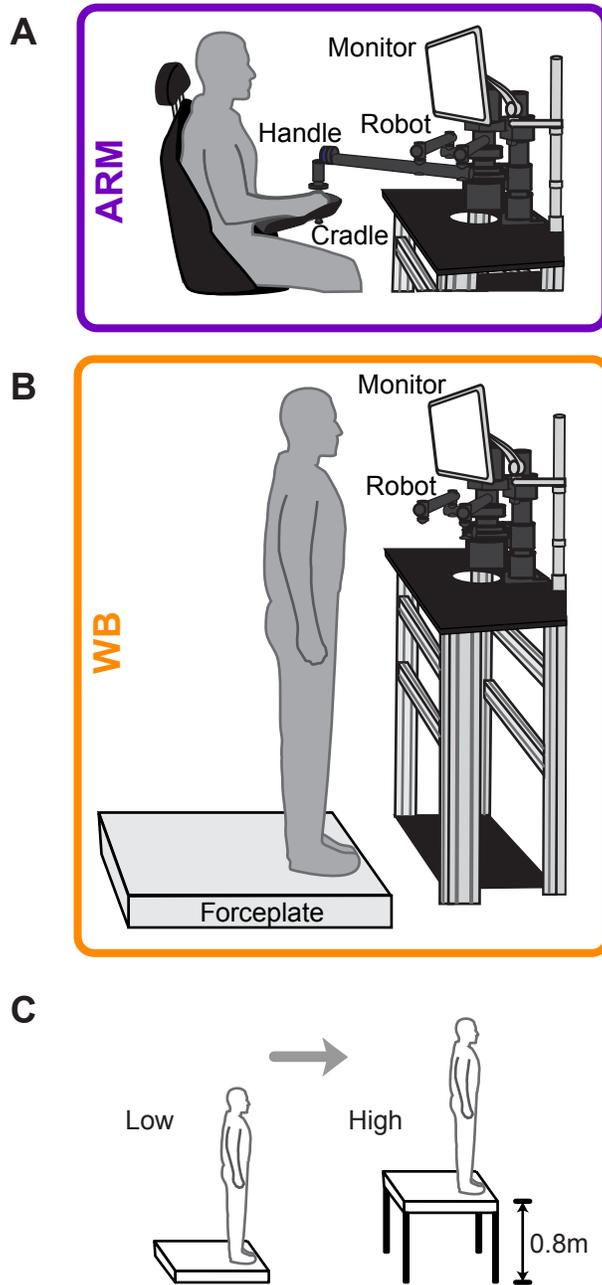


Figure 4.1. Experimental setup for motor tasks. Schematic of (A) arm-reaching task (ARM) and (B) whole-body (WB) movement task. Subjects executed out-and-back movements to a target during training and realization of choices. (C) Subjects performed all movement and choice tasks at ground level (Low elevation) and then at the edge of a 0.8m platform (High elevation).

Lottery design

Construction of lottery pairs is based on the design of Wu et al. (2009) and follows what we implemented in O'Brien and Ahmed (2014). Subjects were asked to choose between two lotteries (A and B), each of which had a different monetary reward ($\$y$ and $\$z$) and probability of winning that reward (p and q). Let us formulate these lotteries as $A(\$y, p)$ and $B(\$z, q)$. For every trial, there was one “safer” lottery and one “riskier” lottery, classified based on the variance of each lottery. We consider the lottery with a higher variance to be the riskier option.

$$\begin{aligned}\text{Var}[A] &= py^2(1-p) \\ \text{Var}[B] &= qz^2(1-q)\end{aligned}\tag{4.1}$$

Lottery pairs were presented in three blocks of 24 trials, for a total of 72 trials per task. Each lottery pair consisted of a reference lottery and a varying lottery. The reference lottery was fixed within a block, whereas the varying lottery changed on each trials. We used a 4x4 outcome-probability matrix to construct the lottery pairs, as shown in Figure 4.2A. All reference lotteries had the same expected value. For the varying lottery, there were four possible monetary outcomes ranging from \$2.40 to \$48, and there were four possible probabilities ranging from 0.05 to 0.95. The diagonal elements of the matrix had nearly the same expected value and were shown three times per block, while the remaining off-diagonal elements were shown once per block. For each subject and task, we randomized the order of the blocks and the order of the varying lotteries within each block.

An example lottery pair for the ARM choice task is shown in Figure 4.2B. In both motor tasks, subjects were shown monetary rewards and targets of varying widths, but they were not told which lottery was riskier or safer on any given trial. We constructed the target sizes to correspond to certain probabilities of hitting the target. We measured subjects' mediolateral endpoint variability during the ARM and WB training tasks, and we use these variabilities to construct motor lotteries that are equivalent to economic lotteries with explicit probabilities.

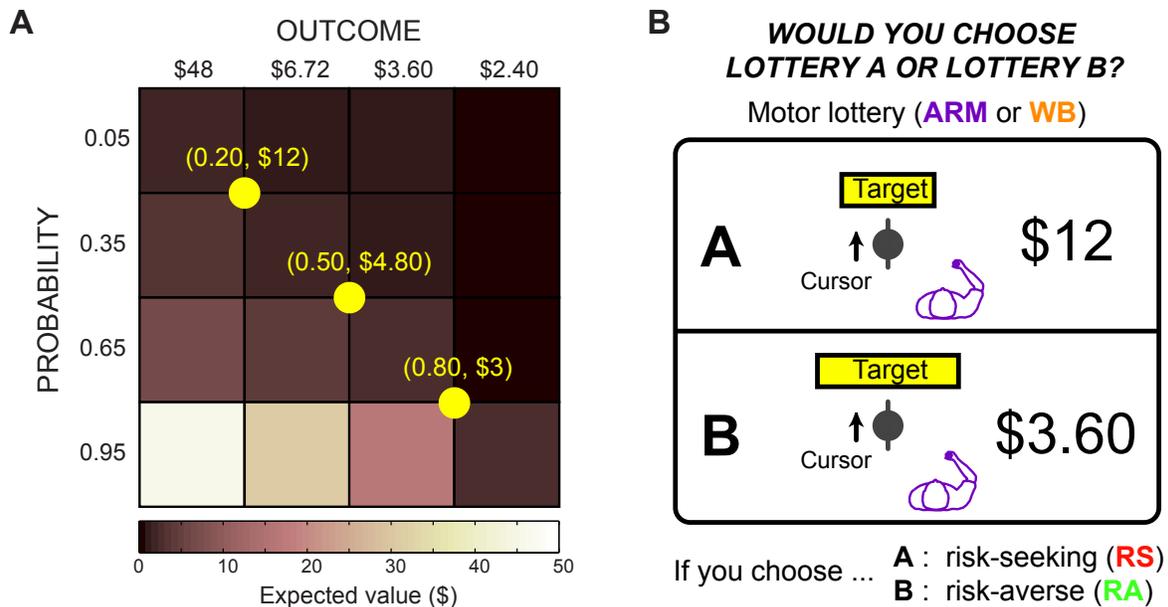


Figure 4.2. Motor lotteries. (A) Presentation of a motor lottery included a target with some width and a monetary reward for hitting that target. Arrow indicates desired direction of cursor movement. Horizontal cursor position at target determines whether the subject would win the reward. (B) Lotteries were constructed using a 4x4 outcome-probability matrix, where each block is paired with each reference lottery (shown in yellow).

Variability testing and motor lotteries

Prior to the testing phase, subjects had the opportunity to perform practice movements for both the ARM and WB tasks. They performed 100 trials at a prescribed time (750-850 ms) to a thin target line, receiving visual feedback regarding their mediolateral proximity to the center of the target. The target line was located at a single distance for all trials within each movement task (12cm for ARM and 6cm for WB). In the realization of choices phase, the target was located at these same distances.

We used the mediolateral standard deviation of the cursor at the target line, σ , to construct the motor lottery target sizes for testing. That is, we adjusted the width of the target during testing so that the subject's probability of hitting the target had an approximate value. From Wu et al. (2011), the relationship between the probability of hitting a target, p_{target} , and the width of a target for motor lottery, w , is:

$$p_{\text{target}} = \int_{x_0 - 0.5w}^{x_0 + 0.5w} \frac{1}{\sqrt{2\pi\sigma^2}} e^{-(x-x_0)^2/2\sigma^2} dx, \quad (4.2)$$

where x is the horizontal axis, and x_0 is the center of the target

Measures of risk-sensitivity

We employed cumulative prospect theory (CPT) to estimate subject-specific distortions in the utilities and probabilities associated with our lotteries. In CPT, risk-sensitivity can be explained by a distortion in (1) the utility/value function or (2) the probability weighting function (Tversky and Kahneman 1992). For our lottery task, we employ CPT to model the subjective value function of monetary rewards $v(O)$ and probability weighting $w(P)$ as:

$$v(O) = O^\alpha, \quad O \geq 0 \quad (4.3a)$$

$$w(P) = \exp[-(-\ln(P))^\gamma], \quad 0 < P < 1 \quad (4.3b)$$

Parameters for utility and probability weightings are α and γ , respectively.

Distortions in utility and probability ($\alpha, \gamma \neq 1$) characterize risk-sensitive behavior, with $\alpha < 1$ and $\gamma < 1$ indicative of risk-aversion and overweighting of small probabilities, respectively. Conversely, $\alpha > 1$ and $\gamma > 1$ are indicative of risk-seeking behavior and underweighting small probabilities, respectively.

The cumulative prospects of the two lotteries, A(\$y, p) and B(\$z, q), are:

$$\begin{aligned} \psi_A &= v(y)w(p) \\ \psi_B &= v(z)w(q) \end{aligned} \quad (4.4)$$

We implemented a logistic choice function with constant noise, so the probability that a subject chooses lottery A is given by:

$$P_A = \frac{1}{1 + \exp[-k(\psi_A - \psi_B)]}, \quad (4.5)$$

where k is a parameter that accounts for stochasticity in a subject's choices. A stochasticity parameter $k=0$ characterizes random choice.

Maximum likelihood estimation was then used to estimate subject-specific distortions in utility and probability for each task. On the i th trial, a subject makes a choice r_i . Let $r_i = 1$ denote choosing lottery A, and let $r_i = 0$ denote choosing lottery B. Our estimated parameters (α, γ, k) for each subject and task maximized the likelihood function over n trials:

$$L(\alpha, \gamma, k) = \prod_{i=1}^n P_A^{r_i} (1 - P_A)^{1-r_i}. \quad (4.6)$$

We used MATLAB's *fminsearch* function with multiple restarts to minimize the negative value of this likelihood function. We compared the resulting parameter fits from this risk-sensitive model with those from other potential models, including a risk-neutral model for each subject (with $\alpha=\gamma=1$ and k left as a free parameter), a risk-sensitive model using random choices as the input, and a risk-sensitive model with a scaling factor on the standard deviation of movement endpoints ($\sigma' = c\sigma$,

where c is a free parameter) to account for potential distortions in subjects' perceptions of their own motor variability.

As another measure of risk-sensitivity, we computed subjects' frequency of risky choices (fR) in each task. The fR metric is determined as a ratio of the number of trials for which a subject chose the riskier lottery over the safer lottery to the total number of trials in a task. Although this metric does not provide information about risk preferences on individual trials, it provides global view of risk-seeking (or risk-averse) behavior that we can use to broadly compare across conditions.

Skin conductance

We measured changes in skin conductance throughout this experiment using the BIOPAC MP35 acquisition hardware, collecting data at 1000 Hz. Disposable electrodes were placed on the subject's left hand, on the distal phalanx of the index and middle fingers. Skin conductance level (SCL) for each subject was calculated as a percent increase over a baseline condition, during which subjects sat quietly for 5 minutes. SCL data is available for 19 of the 20 subjects; one subject's SCL data is not presented due to a calibration error.

Data acquisition

In the ARM training task, optical encoders sample the position of the robot handle at 200 Hz. In the WB training task, the dual-top force platform is comprised of two separate force plates (one for each foot) and records eight analog voltage

signals for each plate, which we use to compute three-dimensional forces (F_x, F_y, F_z) and moments (M_x, M_y, M_z) about the center of each plate at 200 Hz. Center of pressure (COP) for each plate was calculated relative to the center of the dual-top forceplate, $[C_x C_y]$, as $[COP_x COP_y] = [C_x C_y] + [M_x M_y]/F_z$, where x and y refer to mediolateral and anteroposterior axes, respectively. We calculate the combined COP as a weighted average of the COP for each plate (Winter 1996).

Statistics

We used paired t-tests to compare SCL between the arm-reaching and whole-body movements and between the Low and High elevations. We used one-sided paired t-tests to examine potential differences in CPT parameter fits and in fR between postural threat conditions, against the alternative hypothesis that mean values at High elevation were lower than those at Low elevation (corresponding to increased risk-aversion with postural threat). We used two-sided paired t-tests to examine potential differences in CPT parameter fits and in fR between motor tasks. Permutation testing was also employed to compare CPT parameter fits between conditions without making assumptions about the underlying distribution of the samples. We used a one-sided paired t-test to compare scaling factors c on perceived motor endpoint deviation between tasks, against the post-hoc alternative hypothesis $c_{WB\ Low} < c_{ARM\ Low}$. Using the Akaike information criterion (AIC), we compared likelihoods of the full risk-sensitive CPT model (with 3 free parameters) to those of a risk-neutral model (using k as the only free parameter), and we also compared

likelihoods of the full risk-sensitive model (computed using actual subject choices) to those of a risk-sensitive model using random choices. We additionally used AIC to compare likelihoods of the full risk-sensitive model (with 3 free parameters) to those of the risk-sensitive model that included the scaling factor on σ (resulting in 4 free parameters). For all statistical tests, the significance level was set to 5%. Unless otherwise stated, mean values are presented as mean [\pm SEM].

4.3 Results

Overview

Both postural threat and motor task impacted risk-sensitivity. The effect of threat on movement decisions is evident from CPT model fits: increased elevation resulted in greater overweighting of small probabilities for whole-body movement decisions but did not affect arm-reaching decisions. The effect of motor task on decisions emerges from differences in frequency of risky choices: subjects chose riskier lotteries more often in the whole-body task than in arm-reaching at low elevation. We believe the disparate risk-sensitivity between motor tasks could manifest from an underestimation of endpoint variability in the whole-body movement.

Individual subjects' endpoint variability in each task and condition is provided in the supplemental information.

Postural threat increases physiological arousal

To determine whether the increased elevation led to changes in physiological arousal, we compared SCL across conditions. Mean SCL for the Low and High elevation conditions in each motor task are given in Figure 4.3. For each condition, SCL was significantly higher than at Baseline ($p < 0.001$). Increasing elevation led to significantly higher skin conductance levels above the baseline condition in both ARM and WB tasks ($p < 0.001$), indicating that subjects responded physiologically to this form of postural threat. There were no significant differences between the two motor tasks within elevation conditions (Low: $p = 0.73$; High: $p = 0.99$).

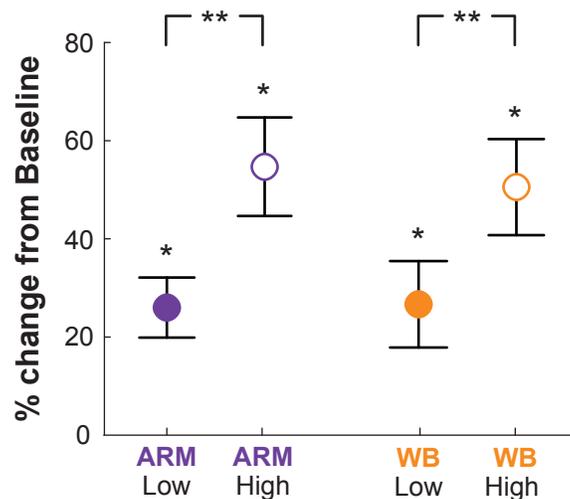


Figure 4.3. Skin conductance. Skin conductance levels (SCL) for all threat conditions relative to Baseline (quiet sitting). SCL at both elevations was significantly higher than at Baseline (* $p < 0.001$), and SCL at the High elevation was significantly higher than at the Low elevation (** $p < 0.001$).

Postural threat affects decisions for whole-body movements, but not for arm-reaching

Median CPT parameter fits and 95% confidence intervals, taken across all subjects, are given in Table 4.1 and illustrated in Figure 4.4. For both ARM and WB, these median fits correspond to exponentially decaying utility ($\alpha < 1$) and a tendency to overweight small probabilities in the Low and High elevation conditions ($\gamma < 1$). In accordance with the fourfold pattern of risk attitudes implicated in cumulative prospect theory (Tversky and Kahneman 1992), greater overweighting of small probabilities corresponds with more risk-seeking behavior for small-probability gains and more risk-averse behavior for small probability losses. In the context of movement control, successful target acquisition can be considered a gain, while movement errors are synonymous with losses. Thus, a concave utility function and the direction of the median probability weighting functions suggests increased risk-aversion toward movement errors at High elevation.

Table 4.1. Median CPT parameter fits (all subjects). Median α , γ , and k values with 95% confidence intervals. Asterisk (*) indicates a significant difference from Low elevation within motor task ($p < 0.05$).

	α	γ	k
ARM Low	0.68 [0.34, 0.88]	0.97 [0.81, 1.06]	5.23 [3.75, 7.42]
WB Low	0.72 [0.29, 0.96]	0.99 [0.75, 1.06]	4.97 [1.82, 9.03]
ARM High	0.53 [0.29, 0.87]	0.90 [0.67, 1.15]	7.35 [4.08, 19.36]
WB High	0.49 [0.36, 0.92]	0.82* [0.46, 1.06]	4.97 [2.57, 15.21]

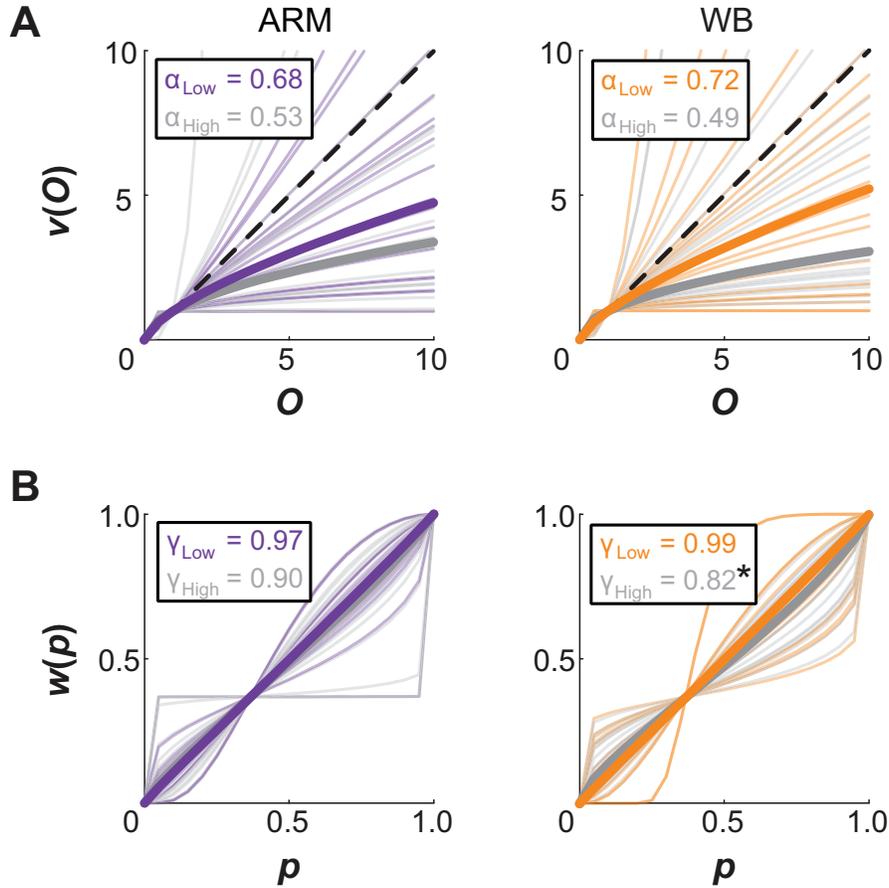


Figure 4.4. CPT curves. Cumulative prospect theory (CPT) model fits for (A) utility and (B) probability weighting in the ARM and WB tasks. Thick lines indicate the median curves for Low elevation (colored) and High elevation (gray); thin lines correspond to fits for individual subjects. Probability weighting parameter γ is significantly lower in WB High than in WB Low (* $p < 0.05$), suggesting that there is a greater distortion in probability representation under increased threat for the WB task.

We used permutation testing to construct an empirical distribution of the difference between the median parameters, thereby making no assumptions about the distribution of these parameters. This method revealed that γ values in WB High are significantly smaller than those in WB Low ($p < 0.05$), which was also supported by a paired t-test. There was no significance between α or γ parameters for any other comparison between motor tasks or between elevation conditions.

Frequency of risky choices reveals differences between motor tasks

A comparison of elevation-based changes in SCL with elevation-based changes in fR yielded a moderate positive correlation in the WB task ($\rho = 0.60$, $p < 0.01$), so greater physiological arousal at high elevation was correlated with more risk-seeking behavior. There was no correlation between elevation-based changes in SCL and elevation-based changes in fR for the ARM task, so increased physiological arousal was not related to fR in this motor task.

Figure 4.5A illustrates average fR for each motor task and elevation. At Low elevation, average fR is greater in the WB task than in the ARM task ($p < 0.02$; ARM Low: 0.56 [0.03], WB Low: 0.62 [0.04]). At High elevation, however, there is no significant difference in fR between the two tasks ($p = 0.25$; ARM High: 0.58 (0.04), WB High: 0.62 [0.04]).

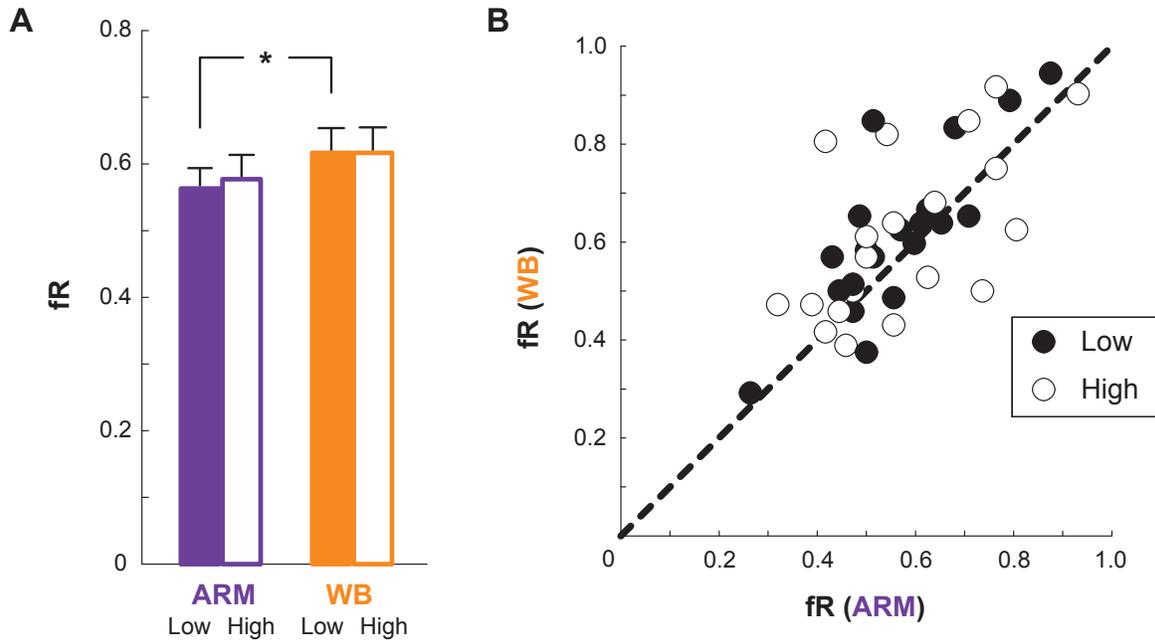


Figure 4.5. Frequency of risky choices. (A) Mean frequency of risky choices (fR) for ARM and WB at Low elevation (filled bars) and at High elevation (outlined bars). (B) Each subject's fR in the ARM condition compared with that in the WB condition, at Low elevation (filled circles) and at High elevation (outlined circles). A data point on the line of unity indicates that the subject chose the same number of risky lotteries in both motor tasks.

From Fig. 4.5A, the mean fR at High elevation is greater than (as in ARM) or equal to (as in WB) the mean fR at Low elevation. We should note, however, that an outlier appears to primarily drive this trend. That is, one subject dramatically increased fR going from Low to High elevation in both motor tasks. This subject's ΔfR between elevations fell outside the interquartile range for both ARM and WB tasks. Upon removing this subject, the fR means are 0.58 (0.03) for ARM Low, 0.63 (0.03) for WB Low, 0.58 (0.04) for ARM High, and 0.60 (0.04) for WB High, making the mean fR at High elevation equal to (as in ARM) or less than (as in WB) the mean fR at Low elevation. So although Figure 4.5A suggests that mean fR increases

slightly, or stays the same, with elevation, removing an outlying subject establishes, visually, that mean fR actually decreases slightly, or stays the same, with elevation. We repeated all analyses with this outlier subject removed; however, there is no resulting change in our statistical outcomes, nor do our overall findings differ with the exception of the aforementioned trends of mean fR compared between Low and High elevations. Thus, we included the outlying subject for the remainder of the analysis presented here.

A comparison of individual fR values between the two motor tasks are shown in Figure 4.5B for both Low and High elevations. Here, a data point on the line of unity indicates an identical fR between the two motor tasks at that elevation, while a data point above unity represents someone who was more risk-seeking in the WB task compared with the ARM task, and a data point below unity represents someone who was more risk-seeking in the ARM task compared with the WB task. There is a smaller variance in the difference between ARM and WB fR at Low elevation ($\sigma_{\text{fR Low}}^2 = 0.0091$) than at High elevation ($\sigma_{\text{fR High}}^2 = 0.022$). That is, at Low elevation, most subjects have a WB fR that is nearly equal to or greater than their ARM fR, illustrating a relatively consistent increase in risky choices during the WB task compared with the ARM task. But at High elevation, there is a much wider range of differences in individuals' fR between the two motor tasks, with some subjects becoming more risk-seeking in the WB task and others becoming more risk-seeking in the ARM task. This explains why we see a significantly higher fR in

the WB task at Low elevation, but there is no significant difference in fR between the paired motor tasks at High elevation.

Generally, subjects' risk preferences appeared to change idiosyncratically between movements and threat conditions. This result is further emphasized in Figure 4.6, which charts individual differences in fR between Low and High elevation conditions for both motor tasks. While some subjects increased fR (becoming more risk-seeking) in both tasks, and others decreased fR (becoming more risk-averse) in both tasks, still other subjects increased fR in one motor task and decreased it in the other motor task.

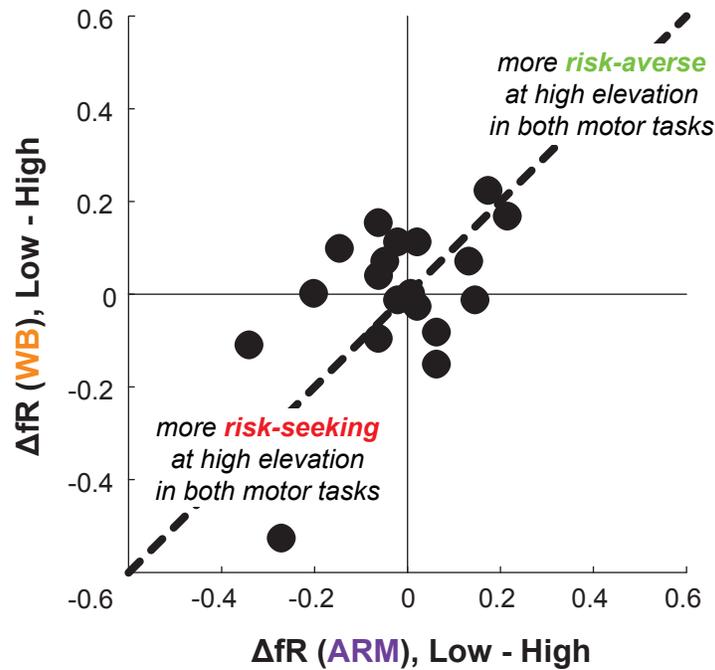


Figure 4.6. Difference in frequency of risky choices between elevations. Each subject’s elevation-based change in fR for the ARM task compared with the WB task. A positive ΔfR corresponds to a subject who had a higher fR at Low elevation than at High elevation, thusly becoming more risk-averse with increasing elevation. A value along the line of unity corresponds to an identical ΔfR in the WB task as in the ARM task, whereas a value above the line of unity, for example, corresponds to having a greater change in risk-sensitivity in the WB task than in the ARM task.

Underestimating motor variability increases fR

Perception of motor variability may also influence choice behavior, since we do not explicitly show subjects the probability that they will hit a given target. For example, if subjects believe themselves to be more accurate than they actually are, they would perceive their probabilities of hitting the target to be higher than those listed in Figure 4.2A. Conversely, if subjects believe themselves to be less accurate

than they actually are, they would perceive themselves to have lower probabilities of hitting the targets (Fig. 4.7A). These perceived values of p_{target} , determined from (4.2) according to an alternate standard deviation of movement endpoints ($\sigma' < \sigma$ or $\sigma' > \sigma$), would replace the probabilities used to calculate cumulative prospects in (4.4).

We next simulated how perceived probabilities, arising from σ' , would affect frequency of risky choices. For each trial, a simulated subject chooses the lottery with a higher expected value, computed using the perceived probabilities. If the selected lottery is also riskier according to the original (undistorted) probabilities, then the number of risky choices increments. Figure 4.7B compares fR for numerous values of σ' . Underestimating motor variability ($\sigma' < \sigma$; thinking you are more accurate than you actually are) results in higher fR, whereas overestimating motor variability ($\sigma' > \sigma$; thinking you are less accurate than you actually are) results in lower fR. This analysis verifies that distorted perceptions of endpoint variability influence choice behavior, and may in part explain why subjects choose riskier lotteries in the WB task.

We ran our CPT model with a scaling factor on σ as an additional free parameter ($\sigma' = c\sigma$). Maximum likelihood estimation fits for this model did not appreciably affect median values of α or γ . The resulting fits for c were not significantly different from 1 in any task or elevation condition. In light of the finding that subjects chose risky lotteries more often in the WB task at Low elevation, we also tested the post-hoc alternative hypothesis that $c_{\text{WB Low}} < c_{\text{ARM Low}}$.

The idea that smaller estimates of motor variability lead to increased fR is substantiated by the simulation shown in Figure 4,7. However, a one-tailed paired t-test fails to reject the null hypothesis that there is no difference between $c_{WB\ Low}$ and $c_{ARM\ Low}$ ($p=0.74$).

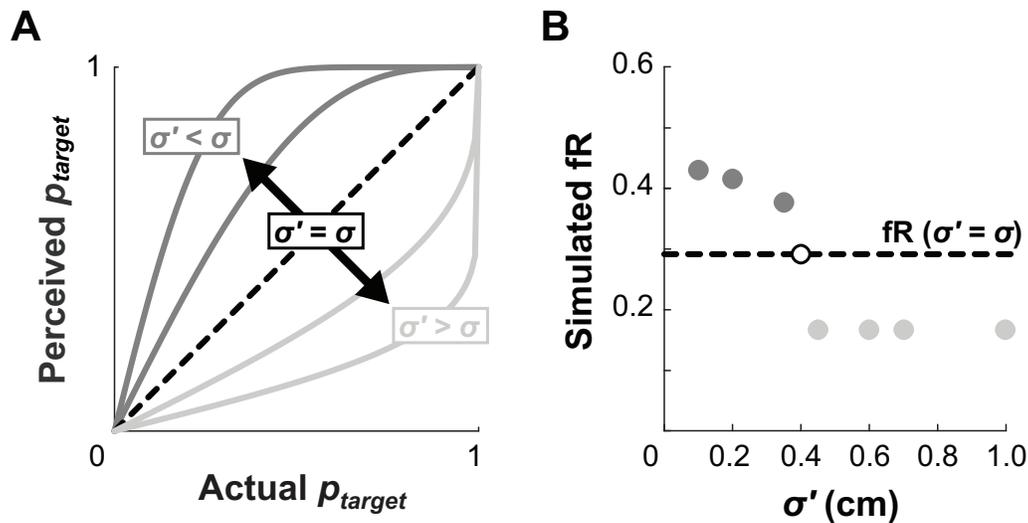


Figure 4.7. Perceived motor variability affects fR. (A) If a subject holds an inaccurate perception of the standard deviation of their endpoints (dark grey: $\sigma' < \sigma$; or light grey: $\sigma' > \sigma$), they will have a distorted perception of the probability they will hit a target in accordance with (2). This distortion would effectively alter the lottery probabilities shown in Fig. 2A according to their perceived p_{target} . (B) Inaccurate perceptions of σ would hypothetically affect subject choices. Believing yourself to be *more* accurate than you actually are (dark grey: $\sigma' < \sigma$) would *increase* fR, while believing yourself to be *less* accurate than you actually are (light grey: $\sigma' > \sigma$) would *decrease* fR. In this example, the simulated subject has $\sigma=0.40$ cm, but the pattern of σ' affecting fR holds across values of σ .

Exploration of alternate CPT models

To examine the fidelity of our parameter fits, we computed the Akaike information criterion (AIC) from the maximum likelihood of the model. Preferred models are those with minimum AIC values. We compared the AIC for the risk-sensitive (full) CPT model with 3 free parameters against a risk-neutral (null) model with α and γ set to unity and with k as the single free parameter. The risk-sensitive model had a lower AIC than the risk-neutral model for all subjects; on average, $AIC_{\text{full}} = 44.8$ and $AIC_0 = 77.5$. We also compared the AIC for the risk-sensitive model with actual subject choices against a risk-sensitive model with random choices. We generated 100 sets of random choices for each subject and task and used the maximum likelihood of these sets to calculate an AIC value for the random choice model. The model with actual subject choices had a lower AIC for all subjects than a model with random choices; on average, $AIC_{\text{rand}} = 109.7$. Thus, a risk-sensitive model is better able to describe subjects' choices, and these choices do not appear to be random. Including a scaling factor on σ , to account for potential distortions in perceived motor variability, did not improve our model fits; on average, $AIC_{\sigma} = 46.1$. Overall, the 3-parameter risk-sensitive model is simpler while maintaining the lowest average AIC. A summary of AIC values for each task and model type is provided in Table 4.2.

Table 4.2. CPT model comparison. AIC values for four iterations of CPT models. The full risk-sensitive model (AIC_{full} , with 3 free parameters) exhibits higher performance.

	AIC_{full}	AIC_0	AIC_{rand}	$AIC_{c\sigma}$
Parameters	3 (fit α, γ, k to subj. choices)	1 ($\alpha=\gamma=1$, fit k to subj. choices)	3 (fit α, γ, k to rand. choices)	4 (fit $\alpha, \gamma, k, c\sigma$ to subj. choices)
ARM Low	47.8	80.6	108.6	47.0
WB Low	43.7	76.3	110.1	47.8
ARM High	43.5	80.5	111.1	44.4
WB High	44.3	72.8	111.6	45.2
Mean	44.8	77.5	109.7	46.1

Within-subject choice consistency

On average, subjects made consistent choices in 89.8% of the lotteries for the repeated task, with most discrepancies lying on the diagonal of the outcome-probability matrix (Fig. 4.2A), immediately adjacent to the presented reference choice.

The trends we found using a CPT analysis also hold when we compare the repeated WB Low task with WB High. That is, using this repeated task, there is still less exponential decay in utility at Low compared to that at High, and an overweighting of small probabilities. Importantly, permutation and paired t-tests still show that γ is significantly greater in this repeated WB Low than in the original WB High. We also saw no significant difference in fR between the original WB Low and the repeated task (paired t-test; $p=0.84$), and there is still a larger fR for the repeated WB Low task than ARM Low (paired t-test; $p<0.001$).

4.4 Discussion

Skin conductance measures confirmed that subjects experienced a physiological response to the postural threat presented in this experiment. Postural threat and motor task both affected movement-based risk preferences. Increasing postural threat in the form of elevation resulted in greater overweighting of small probabilities in the whole-body task, which is consistent with increased risk-aversion toward potential movement errors. We also found that individuals are more risk-seeking in whole-body leaning movements than in arm-reaching at ground level, though this difference in risk preferences between motor tasks cannot be explained solely through consistent distortions in utility or probability weighting.

Irrespective of elevation, the median CPT fits for both motor tasks align overall with risk-seeking behavior for small probability gains and risk-averse behavior for small probability losses, with an exponential decay in utility and overweighting of small probabilities for both motor tasks. These risk preferences contradict the trends found by Wu et al. (2009, 2011) for a pointing task. When comparing choices in a motor lottery to those in a classical economic lottery, these authors found evidence for underweighting of small probabilities in the motor domain and the typical overweighting of small probabilities in the economic domain. A functional magnetic resonance imaging (fMRI) study revealed that subjective utility is encoded in the medial prefrontal cortex (mPFC) and the posterior cingulate cortex (PCC) of the brain. Probability, on the other hand, is represented differently in the mPFC depending on whether it is explicitly presented (as in the

economic lottery) or implicitly presented (as in the motor lottery). Our choice tasks implemented implicit probabilities for both motor tasks and elevations, so we do not expect any observed differences in probability weighting to be confounded by the different neural mechanisms of probability encoding.

In the whole-body task, elevation further distorted probability weighting, with most subjects overweighting small probabilities to a greater extent when standing atop a 0.8m platform than when standing at ground level. With concave utility, this shape of the weighting function agrees with the fourfold pattern of risk attitudes, describing risk-seeking behavior for small-probability gains and risk-averse behavior for small probability losses. In the context of goal-directed movement, we interpret gains as target acquisition and losses as movement errors.

Greater overweighting of small probabilities, then, indicates that subjects adopted a more cautious strategy at high elevation due to overweighting the probability of errors.

Interestingly, subjects only altered probability weighting in the movement that was more pertinent to the imposed postural threat. Successful completion of the whole-body motor task required subjects to lean over the edge of the elevated platform, thereby directly confronting them with the increased threat. Previous studies of postural threat have noted changes in postural control when standing or moving at increased elevations – namely, tighter control of the center of pressure along both the anteroposterior and mediolateral axes, posterior shifts in the center of pressure, and reduced displacement and velocity of the center of pressure and

center of mass during voluntary movement. These postural control changes have been shown to scale with elevation and are more pronounced at platform heights greater than 1.5m (Adkin et al. 2000; Adkin et al. 2002; Adkin et al. 2008; Davis et al. 2009; Cleworth et al. 2012). We anticipate that the observed changes in choice behavior would also scale with elevation, resulting in even greater distortions in probability weighting for the whole-body task.

We introduced postural threat in this experiment without altering the motor tasks, allowing us to directly probe the effect of emotional stress on movement choice behavior. Even in economic decision making, only recently have systematic investigations of stress effects been performed. Mild psychosocial stress, often induced using the Trier Social Stress Test (TSST), appears to disparately affect gains and losses. For example, in a modified Game of Dice Task, Pabst et al. (2013) found that participants did not alter behavior in gains but made fewer risky decisions in losses after performing the TSST. Such behavior supports the idea that elevation would increase risk-aversion in relation to movement errors. Yet, Porcelli and Delgado (2009) observed an opposite effect, with increased risk-taking for losses as well as decreased risk-taking for gains. However, unlike in our experiment, both of these studies provided feedback about the outcome after each choice, which may have contributed to their conflicting findings. Buckert et al. (2014) did not provide trial-by-trial feedback about financial gambling choices, discovering that stress increased risk-taking in the gain domain (linked with cortisol responses) and did not significantly affect risk-taking in losses.

We had previously assessed risk-sensitivity in movement using a continuous motor task, wherein subjects used out-and-back arm-reaching or whole-body leaning movements to maneuver a cursor toward the edge of a virtual “cliff” (O’Brien and Ahmed 2013). They were given a point score for each trial, with higher rewards for traversing closer to the cliff edge and a penalty if the cursor moved beyond the cliff edge. In comparing subject endpoints with a variability-based model of optimal movement planning, we saw that subjects moved closer to the cliff edge than was appropriate for maximizing their expected reward, suggesting risk-seeking behavior. Moreover, subjects were consistently more risk-seeking in the whole-body task than in arm-reaching. However, it was unclear whether this disparity in risk-sensitivity between the two types movement resulted from differences in utility (subjective valuation of the rewards and penalties), differences in distorted probability weighting (where probability is again tied to motor variability), differences in motor costs, or some combination thereof. In the present study, we specifically explored potential differences in probability weighting and utility between these movements using a discrete, choice-based paradigm. Subjects chose riskier options more frequently in the context of the whole-body movement than in arm-reaching at low elevation (ground level), which supports our previous findings. However, from our CPT analysis, there were no significant differences in utility or probability weighting between the two motor tasks at low elevation. Median parameter fits (Fig. 4.4) further illustrate that distortions in utility and probability weighting were indeed very similar between motor tasks within

elevations. Another possible explanation for the dissimilar choice behavior between arm-reaching and whole-body leaning may be in subjects' perceptions of their own motor variability. We demonstrated that underestimating endpoint variability would result in inflated frequency of risky choice. Adjusting our risk-sensitive CPT model to include a scaling factor on endpoint deviation did produce better parameter fits, nor did we find significant differences in the scaling factor between motor tasks. It is likely that a combination of distortions – in utility, probability weighting, and perceptions of motor variability – contribute to the observed choice behavior and effects are difficult to tease out due to between-subject variance. It also remains to be seen whether differences in motor costs or subjective valuation of effort would separately influence risk-sensitivity in the two motor tasks.

It is possible that some perceived changes in risk preferences between tasks or conditions could result from noise or inconsistencies in individual subjects' choices, rather than from the threat itself. However, subjects repeated one of the motor tasks (whole-body leaning at low elevation) during the experimental session, and were relatively consistent in their choices between the original task and the repeated task. Overall, our findings hold whether we examine the original whole-body task or the repeated task, suggesting that differences between low and high elevations are more likely due to the postural threat, not simply within-condition noise.

This is the first study to investigate changes in movement risk-sensitivity under increased postural threat. It remains unclear at present whether it is possible

to predict individuals' risk-sensitivity in certain movements or emotional states based on their decisions other movements or emotional states. It appears, however, that postural threat does affect risk-sensitivity in movement, and the threat may induce risk-aversion in a salient movement task.

APPENDIX A

RELATION BETWEEN CUMULATIVE PROSPECT THEORY PARAMETERS AND FREQUENCY OF RISKY CHOICE

Median α and γ values are similar between ARM and WB at Low elevation, providing no additional information about consistent distortions that might prompt subjects to choose the risky lottery more often in WB than in ARM, as established by the fR metric. At High elevation, median values are again similar between ARM and WB, but they indicate greater exponential decay of utility compared with Low elevation, as well as greater underweighting of large probabilities.

It is pertinent, then, to directly address how our different risk-sensitivity metrics map onto each other. Particularly, how does a decrease in probability weighting, as seen in the WB task, translate to a change in the frequency of risky choices? For each of the lottery pairs presented in this experiment, we simulated the choices that subject with certain CPT parameters would make. To do so, we selected α and γ values and calculated the resulting cumulative prospect of the lotteries from (4.4). When considering each lottery pair, the simulation then chose the lottery with a higher cumulative prospect, which may or may not be the lottery that is riskier. From the simulation's choices, we tallied the number of riskier lotteries chosen, which gave the fR metric for that set of CPT parameters. It follows then that we can examine how small changes in α and γ affect fR.

From Figure 4.8A, we observe that fR generally increases as α increases, and this pattern holds for different values of γ . For $\alpha < 1$ (exponential decay of utility),

smaller γ values produce larger difference in fR. From Figure 4.8B, we can see that changes in γ have a more complex effect on fR, as fR generally decreases with γ for small γ , but larger γ can result in increased fR. For $\gamma < 1$ (underweighting of large probabilities), smaller α values produce larger changes in fR if $\alpha \geq 1$. Due to the S-shaped and asymmetric nature of the probability weighting function, the specific probabilities given in the lottery pairs will contribute differently to fR. Figure 4.8C replicates the mapping of γ onto fR for a fixed $\alpha = 1$, and it also shows how the value of the riskier lottery's probability contributes to that fR. Thus, changes in gamma have competing effects on low and high probability lotteries. Since in this experiment the distribution of low and high probabilities was approx. even, this likely washed out the effect of a change in gamma on frequency of risky choice.

Going from Low to High elevation, our subjects exhibited a significant decrease in γ for the WB task (median values: $\gamma_{\text{Low}} = 0.99$, $\gamma_{\text{High}} = 0.82$). According to our simulation, this would result in a slightly higher fR for WB High compared with WB Low. Such an effect is not observed in the fR data (as shown in Fig. 4.5, or with the outlying subject removed), as it may be washed out by an accompanying decrease in α at High elevation.

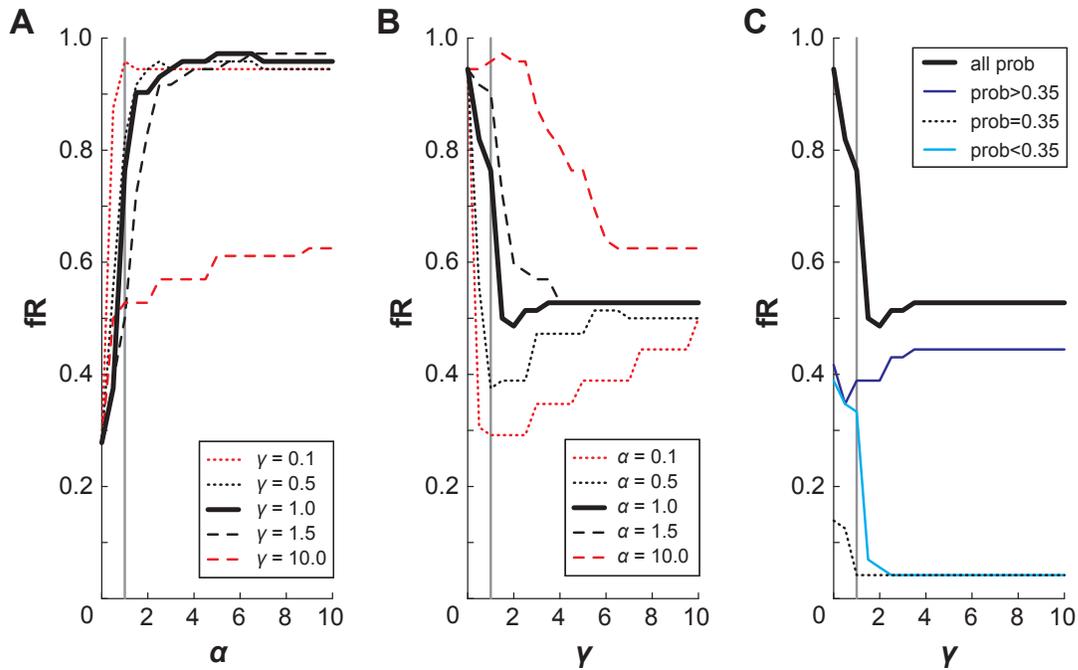


Figure 4.8. Simulation of CPT parameters and resulting fR. Frequency of risky choices computed from values of (A) utility parameter α (shown for various values of γ) and (B) probability weighting parameter γ (shown for various values of α). (C) Due to the S-shaped nature of the probability weighting function, small and large probabilities contribute differently to overall fR (shown for $\gamma=1$).

CHAPTER 5

THE EFFECT OF POSTURE AND POSTURAL THREAT ON ECONOMIC RISK-SENSITIVITY

The work in this chapter is also published as: O'Brien MK, Ahmed AA. Take a stand on your decisions, or take a sit: posture does not affect risk preferences in an economic task. *PeerJ* 2:e475, 2014.

5.1 Abstract

Physiological and emotional states can affect our decision-making processes, even when these states are seemingly insignificant to the decision at hand. We examined whether posture and postural threat affect decisions in a non-related economic domain. Healthy young adults made a series of choices between economic lotteries in various conditions, including changes in body posture (sitting versus standing) and changes in elevation (ground level versus atop a 0.8-meter-high platform). We compared three metrics between conditions to assess changes in risk-sensitivity: frequency of risky choices, and parameter fits of both utility and probability weighting parameters using cumulative prospect theory. We also measured skin conductance level to evaluate physiological response to the postural threat. Our results demonstrate that body posture does not significantly affect decision making. Secondly, despite increased skin conductance level, economic risk-sensitivity was unaffected by increased threat. Our findings indicate that economic

choices are fairly robust to the physiological and emotional changes that result from posture or postural threat.

5.2 Introduction

Have you ever wondered whether you were in the right frame of mind to make a decision? Converging evidence suggests that physiological and emotional states affect decision making, even when these states are not particularly salient to the decision task. For example, a recent study demonstrated that metabolic state can alter risk-sensitivity in an unrelated economic decision-making task, suggesting similar neurobiological correlations for the representation of value and uncertainty across task domains (Symmonds et al., 2010). Another group found that action planning can influence our perceptions (Witt & Brockmole, 2012). When holding a gun, subjects were more likely to perceive objects held by others as guns, and they were more likely to exhibit threatening behavior, such as raising the gun to a shooting posture. When holding neutral objects, such as a ball or a shoe, subjects were more likely to identify objects held by others as neutral objects rather than guns. This outcome appears to support a theory of event encoding, where action planning biases perception (i.e. planning an action involving a gun results in a bias to identify other objects as guns) because action-based and perceptual representations involve shared neural processes. Indeed, there could be many subtle

changes in our bodies or environment that contribute to choices we make under risk.

Previous studies have found physical and neurobiological implications of adopting certain body postures. For instance, standing is less comfortable than sitting, causing more fatigue and particular discomfort in the feet and lower limbs over prolonged period of time (i.e. 90 minutes) (Chester, Rys & Konz, 2002; Drury et al., 2008). Standing is more biomechanically unstable than sitting and is more likely to result in a fall. Standing is also more cognitively loading than sitting, requiring greater attentional demands to maintain the posture (Teasdale et al., 1993; Lajoie et al., 1993; Lajoie et al., 1996). High-power poses – in which the body is open and expansive – increase testosterone and decrease cortisol levels, whereas low-power poses – in which the body is closed and contracted – have the opposite effect (Carney, Cuddy & Yap, 2010). Posture may also influence our perception, performance, and decision-making processes, potentially as a result of the accompanying physiological changes. More comfortable postures can enhance performance in memory tasks (Lipnicki & Byrne 2005; Yardley et al., 2005), while less comfortable positions can improve reaction time (Vercruyssen & Simonton, 1994). Adopting high-power poses for as little as one minute leads to increased feelings of power as well as risk-seeking behavior in a gambling task (Carney, Cuddy & Yap, 2010), congruous with the neuroendocrine profiles that accompany such poses. However, this risk-seeking behavior was found for monetary losses and involved a single lottery, rather than examining a range of monetary amounts and

probabilities. It is unclear whether more neutral, commonplace postures such as sitting or standing would influence risk-sensitivity for monetary gains. In an earlier study of risk-sensitivity for a motor task, we found that subjects were more risk-seeking in a standing whole-body movement than in a seated arm-reaching movement (O'Brien & Ahmed, 2013). Was this difference in risk-sensitivity due to the types of movement, or simply because of the sitting and standing postures? In the present study, we sought to differentiate possible changes in risk-sensitivity due to the postures themselves using a non-motor task.

Postural threat has also been shown to alter our behavior, particularly in the movement domain. There are multiple examples of altered postural control in the context of minimal increases in postural threat: forward vs. backward leaning (Manista and Ahmed, 2012), standing with a narrow vs. a wide stance width (Piencak-Siewert et al, 2014), and standing on a reduced base of support (Huang and Ahmed, 2012). Modest changes in elevation induce marked changes in motor control and physiological arousal, indicating greater anxiety (Ashcroft et al., 1991; Brown et al., 2002; McKenzie & Brown, 2004; Brown et al., 2006; Brown, Polych & Doan, 2006). When asked to walk or simply stand on an elevated platform, both young and old adults reduce the velocity and extent of their movements (Adkin et al., 2002; Carpenter et al., 2006; Adkin et al., 2008; Davis et al., 2009; Lamarche et al., 2009). During quiet standing, postural control variables are scaled to surface height, with center of pressure (COP) displacements decreasing in amplitude and increasing in frequency at higher elevations, up to 1.6m but as low as 0.81m

(Carpenter, Frank & Silcher, 1999; Adkin et al. 2000; Carpenter et al., 2001). At a surface height of 0.81m, individuals adopt a stiffening strategy during quiet standing, increasing activity in anterior leg muscles and shifting their COP away from the surface edge (Carpenter et al., 2001). Typically, these changes are attributed to a fear of falling that affects the action selection process of the central nervous system (CNS). If changes in movement tasks on elevated platforms are a result of the feelings of threat experienced while standing on the platform, then it is feasible that these emotions will influence risk-sensitive behavior in non-motor tasks as well.

Together, these findings compel us to further examine the effects of physiological and emotional state on decision making. Here we specifically studied the influence of body posture and postural threat on economic decisions. Subjects performed a two-alternative forced choice lottery task under various conditions. We compared their risk preferences across two body postures (sitting vs. standing) and two levels of postural threat in the form of elevation (ground level vs. atop a 0.8m platform). We expected that the more uncomfortable body posture (standing) and higher postural threat (atop the platform), would lead to more risk-averse choices during economic decision making. This conjecture is predominantly based on preceding investigations of the role of affect in judgment and decision making, which suggest that our actions are often based on avoiding negative emotions (Slovic, 1987; Finucane et al., 2000; Loewenstein et al., 2001; Slovic et al., 2002; Loewenstein & Lerner, 2003; Slovic et al., 2004). Because standing induces relative

discomfort, biomechanical instability, and attentional demands, and because elevation magnifies a fear of falling, we anticipated that subjects' desire to avoid such negative states would contribute to a desire to avoid of risk that would carry over to the economic domain. If risk-sensitivity were altered by even subtle changes in feelings of discomfort or threat, this would further assert that consideration of state is fundamental to the ability to mechanistically predict decisions across domains. Conversely, similar risk-sensitivity between conditions would indicate that economic choices bear a level of resistance to physiological and emotional changes.

5.2 Materials and Methods

Ethics statement

All subjects provided written informed consent before participation. The experimental protocol (12-0458) was approved by the Institutional Review Board of the University of Colorado Boulder in accordance with federal regulations, university policies, and ethical standards regarding human subject research.

Experimental protocol

Thirteen healthy subjects (8 females, 5 males; mean age, 23.1 ± 2.2 years) participated in this experiment. These subjects were part of a broader study

examining the influence of threat on non-motor and motor tasks. Subjects made choices in an economic lottery series in four conditions: sitting at low elevation (SIT Low), standing at low elevation (STAND Low), sitting at high elevation (SIT High), and standing at high elevation (STAND High). Throughout a series, subjects were asked to choose between two lotteries, where each lottery has a different monetary reward and probability of winning that reward.

For the Low conditions, subjects either sat in a chair or stood at the edge of a forceplate (AMTI Dual-Top AccuSway, which is 4.5cm in height). For the High conditions, subjects sat in the same chair or stood on the same forceplate at the edge of an elevated platform, 0.8m off the ground. The height of this platform was equivalent to that of an average table or desk, and it is approximately the average height at which young adults perceive they would not be able to use a step down strategy to descend from an elevated surface (Brown & Frank, 1997). When standing in either elevation condition, subjects were secured in a harness and fall protection system that could arrest a fall before the subjects' knees touched the platform. However, to maintain perceptions of postural threat in the presence of this added safety, there was enough slack to the harness to allow subjects to move without restraint, and they were not allowed to explore the competence of the fall protection system before testing.

Subjects performed the SIT and STAND lottery tasks in a randomized order at each elevation, counterbalanced across the two tasks. They completed both choice tasks at Low elevation before performing them at High elevation. Previously, it was

shown that increasing elevation results in more pronounced changes to postural control variables than decreasing elevation (Adkin et al., 2000). In presenting the Low elevation condition first, we intended to capitalize on these order effects to maximize changes in postural control due to threat and, thus, to maximize potential changes in the action selection process.

Lotteries were displayed on a computer monitor in front of the subject. In the testing phase of the experiment, subjects simply chose between pairs of lotteries using a two-button remote. Subjects performed 72 choice trials for each condition, where every choice completed a single trial. Lottery information for each trial was shown for 4 seconds; the lotteries then disappeared and subjects were given 2 seconds to select their preferred lottery. There were no failed trials; all subjects provided a response to every trial.

After completing the four conditions, subjects participated in a realization of choices phase. We randomly selected one trial from each condition, and the subject “played” their choice on that trial for real money. We used a random number generator to determine whether a subject won the monetary reward presented in that choice. Subjects were aware of the random selection of trials to be played in order to ensure their decisions were representative of what they would do in a real-life scenario.

Lottery design

We adapted a lottery series design from Wu, Delgado & Maloney (2011). Subjects chose between two lotteries (A and B), each of which had a different monetary reward (\$ y and \$ z) and probability of winning that reward (p and q). We formulated these lotteries as $A(\$y, p)$ and $B(\$z, q)$. For every trial, there was one “safer” lottery and one “riskier” lottery, which were classified based on the variance of each lottery. The lottery with a higher variance was considered the riskier option.

$$\begin{aligned}\text{Var}[A] &= py^2(1 - p) \\ \text{Var}[B] &= qz^2(1 - q)\end{aligned}\tag{5.1}$$

Lottery pairs were presented in three blocks of 24 trials, for a total of 72 trials per task. Each lottery pair consisted of a reference lottery and a varying lottery. The reference lottery was fixed within a block, whereas the varying lottery changed from trial to trial. We used a 4x4 outcome-probability matrix to construct the lottery pairs, as shown in Figure 1A. The reference lotteries had the same expected value. For the varying lottery, there were four possible monetary outcomes ranging from \$2.40 to \$48, and there were four possible probabilities ranging from 0.05 to 0.95. The diagonal elements of the matrix had nearly the same expected value and were shown three times per block, while the remaining off-diagonal elements were shown once per block. We randomized the order of the blocks as well as the order of the varying lotteries for each subject and task. An example lottery pair is shown in Figure 1B. Subjects were explicitly shown the rewards and

probabilities for each lottery, but they were not told which lottery was safer or riskier on any given trial.

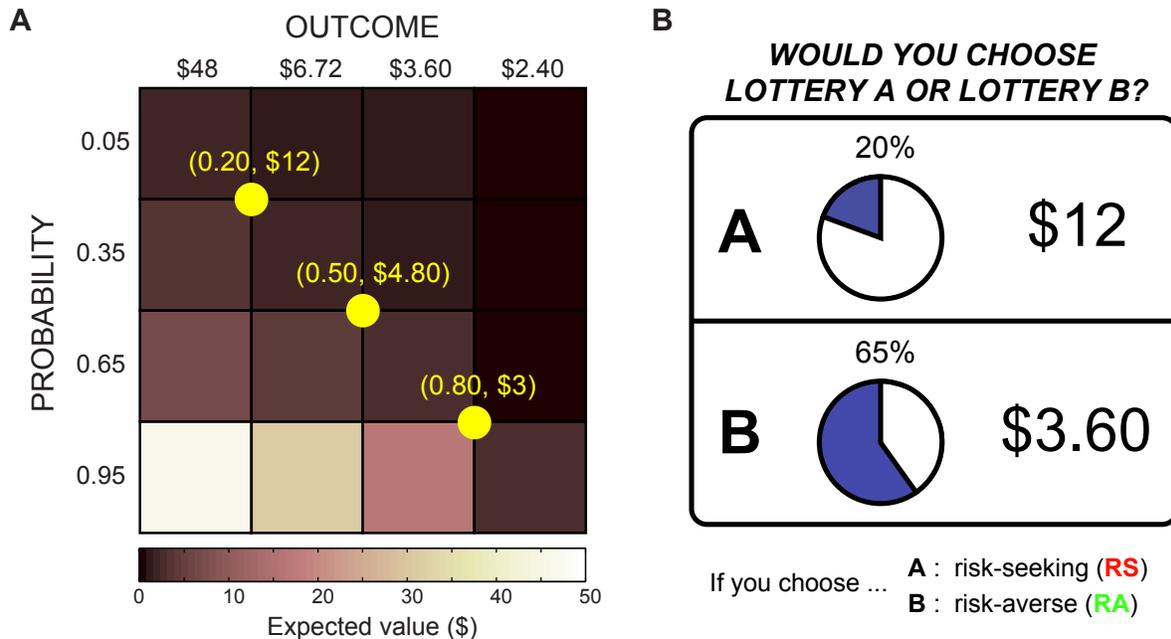


Figure 5.1. Lottery design. (A) Lotteries were constructed using a 4x4 outcome-probability matrix, where each block is paired with each reference lottery (shown in yellow). (B) Sample lottery presentation. Subjects were asked to choose between two economic lotteries, with differing monetary rewards and probabilities of winning those rewards.

Measures of risk-sensitivity

One metric we used to compare risk-sensitivity between conditions was the frequency of risky choices (fR) in each task. We computed fR by comparing how many times a subject chose the riskier lottery over the safer lottery to the total number of trials in a task. Although this metric does not provide information about

risk preferences on individual trials, it provides global view of risk-seeking (or risk-averse) behavior that we can compare across conditions.

We also employed cumulative prospect theory (CPT) to estimate subject-specific distortions in the utilities and probabilities associated with our lotteries. In CPT, risk-sensitivity can be explained by either a distortion in the (1) utility/value function or (2) probability weighting function (Tversky & Kahneman, 1992). Utility refers to the subjective valuation of an outcome (such as money), and a utility function describes how that valuation changes across outcomes. For instance, people tend to perceive the difference between \$5 and \$10 as more meaningful than the difference between \$105 and \$110, even though the objective difference is \$5 in both cases. This is an example of diminishing sensitivity to increasing outcomes and can be captured by modeling utility with a power function. Probability weighting relates the likeliness of an outcome to the desirability of that outcome. Empirical evidence has shown that individuals weight probabilities nonlinearly, usually overweighting small probabilities (unlikely events) and underweighting large probabilities (likely events).

Under the formalization of CPT, we used the following value function, $v(O)$, and Prelec's probability weighting function, $w(P)$:

$$v(O) = O^\alpha, \quad O \geq 0 \tag{5.2a}$$

$$w(P) = \exp[-(-\ln(P))^\gamma], \quad 0 < P < 1 \tag{5.2b}$$

The relevant parameters for utility and probability weightings are α and γ , respectively. Distortions in utility and probability ($\alpha, \gamma \neq 1$) characterize risk-sensitive behavior, with $\alpha < 1$ and $\gamma < 1$ indicative of risk-aversion and underweighting large probabilities, respectively. Conversely, $\alpha > 1$ and $\gamma > 1$ are indicative of risk-seeking behavior and overweighting large probabilities, respectively.

Then, the cumulative prospects of the two lotteries, A(\$y, p) and B(\$z, q), are:

$$\begin{aligned}\psi_A &= v(x)w(p) \\ \psi_B &= v(y)w(q)\end{aligned}\tag{5.3}$$

We used a logistic choice function with constant noise (Stott, 2006; Chib et al., 2012), so that the probability that a subject chooses lottery A is given by:

$$P_A = \frac{1}{1 + \exp[-k(\psi_A - \psi_B)]},\tag{5.4}$$

where k is a parameter that accounts for stochasticity in a subject's choices. A stochasticity parameter $k=0$ characterizes random choice.

We used maximum likelihood estimation to estimate subject-specific distortions in utility and probability for each task. The procedure for fitting these CPT parameters is as follows: on the i th trial, a subject makes a choice r_i . Let $r_i = 1$ denote choosing lottery A, and let $r_i = 0$ denote choosing lottery B. A maximum

likelihood estimation of the parameters (α, γ, k) is one that maximizes a likelihood function over n trials, which we write as:

$$L(\alpha, \gamma, k) = \prod_{i=1}^n P_A^{r_i} (1 - P_A)^{1-r_i}. \quad (5.5)$$

We used MATLAB's *fminsearch* function with multiple starting conditions to minimize the negative value of this likelihood function and estimate each subject's parameters.

Skin conductance

Skin conductance measurements are often used as an indicator of anxiety, affective response, and emotional arousal. We measured changes in skin conductance throughout this experiment using the BIOPAC MP35 acquisition hardware, collecting data at 1000 Hz. Disposable electrodes were placed on the subject's left hand, on the distal phalanx of the index and middle fingers. Skin conductance level (SCL) for each subject was calculated as a percent increase over a baseline condition, during which subjects sat quietly for 5 minutes. SCL data is available for 12 of the 13 subjects; one subject's SCL data is not presented due to a calibration error.

Statistics

We used paired t-tests to compare SCL between the sitting and standing postures and low and high elevations. We performed a two-way repeated-measures analysis of variance (ANOVA) to determine whether there were effects of body position or elevation on our first measure of risk-sensitivity, fR. We used paired t-tests to examine potential differences in fR, as well as Fisher's exact test to compare the distribution of subjects with α and γ values greater than 1.0 between conditions. Permutation testing was employed to further compare CPT parameter fits between conditions without making assumptions about the underlying distribution of the samples. For all statistical tests, the significance level was set to 5%.

5.3 Results

Overview

We found no significant differences in risk-sensitivity between any conditions. Subjects chose riskier lotteries as frequently when sitting as they did when standing, and this frequency did not change between low and high elevation. Similarly, we did not see substantial changes in the parameter fits for utility and probability weighting between conditions.

Skin conductance

Mean SCL for the Low and High elevation conditions are given in Figure 2. For each condition, SCL was significantly higher than at Baseline ($p < 0.004$). There was no difference in SCL between SIT and STAND at either elevation (Low: $p = 0.89$; High: $p = 0.96$), though SCL for conditions at High elevation were significantly higher than those at Low elevation ($p < 0.002$). These measurements suggest that subjects did indeed have a physiological response to elevation, but not to body posture.

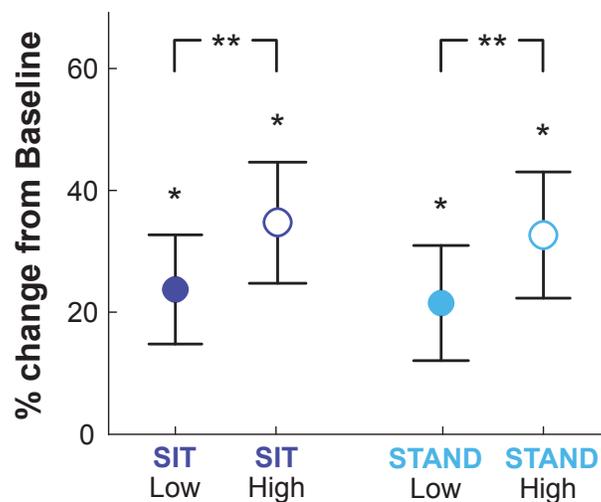


Figure 5.2. Skin conductance. Skin conductance levels (SCL) for all conditions relative to Baseline (quiet sitting). SCL in all conditions was significantly higher than at Baseline (* $p < 0.004$), and SCL at the High elevation was significantly higher than at the Low elevation (** $p < 0.002$). There was no difference in SCL between sitting and standing conditions at either elevation.

Frequency of risky choices

Subjects chose the riskier lottery a comparable number of times regardless of condition. There were no significant differences in average fR between SIT and STAND at either elevation, and fR was similar between the Low and High elevations (Fig. 3A). This figure illustrates a slight, though consistent, trend to choose the risky lotteries less often under higher postural threat, with mean (\pm SEM) fR values of 0.51 (0.05) for SIT Low, 0.49 (0.05) for STAND Low, 0.48 (0.05) for SIT High, and 0.46 (0.05) for STAND High. However, paired t-tests between do not reveal significant differences in fR between any conditions. Figure 3B illustrates that individual fR values in SIT were nearly equal to those in STAND at both Low and High elevations. A repeated-measures ANOVA did not reveal effects of body posture ($F=0.11$, $p=0.74$), elevation ($F=0.26$, $p=0.61$), or an interaction between these factors ($F=0.0011$, $p=0.97$).

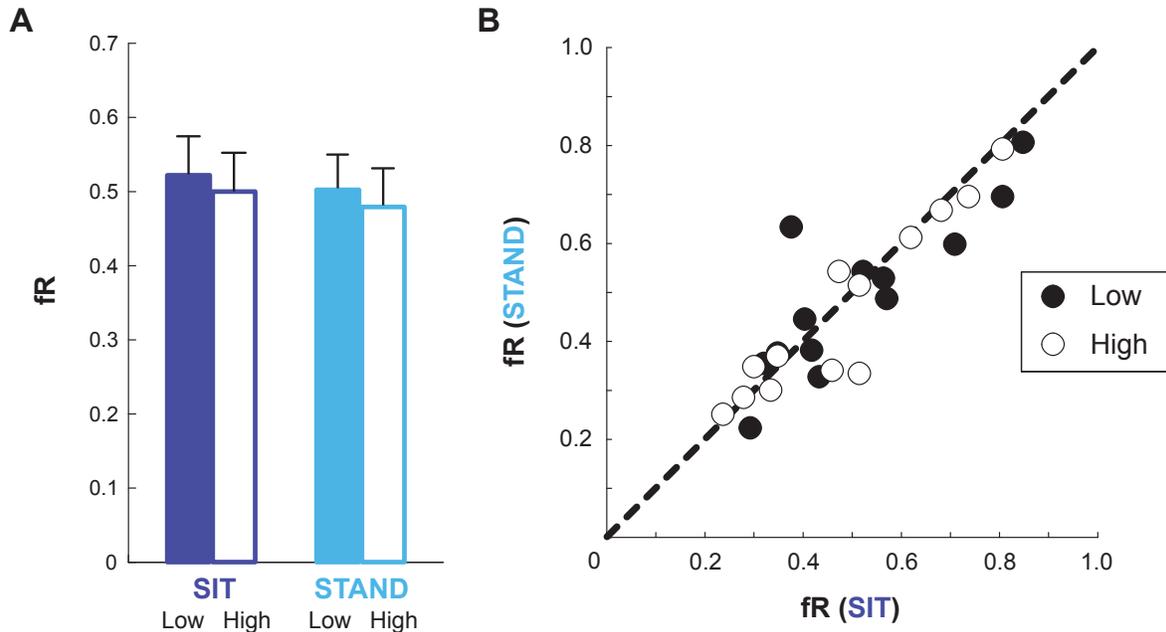


Figure 5.3. Frequency of risky choices. (A) Mean frequency of risky choices (fR) for SIT and STAND at Low elevation (filled bars) and at High elevation (outlined bars). (B) Each subject's fR in the SIT condition compared with that in the STAND condition, at Low elevation (filled circles) and at High elevation (outlined circles). A data point on the line of unity indicates that the subject chose the same number of risky lotteries in both body postures.

CPT parameter fits

Median parameter fits and 95% confidence intervals are given in Table 1. For both SIT and STAND, these median fits suggest risk-averse behavior in utility and a slight tendency to underweight large probabilities (Fig. 5). These trends hold for both elevations. A comparison of individual subjects' CPT parameters between conditions is illustrated in Figure 5. In these plots, if an individual's general risk preferences did not change between the conditions of interest, we would expect data points to fall in the first quadrant (indicating consistent risk-seeking behavior in α

and consistent overweighting of large probabilities in γ) or in the third quadrant (indicating consistent risk-averse behavior in α and consistent underweighting of large probabilities in γ). Such a tendency is particularly evident in utility for both body posture and elevation. Our fits suggest more idiosyncratic behavior in probability weighting between conditions, with a larger number of data points lying in the second and fourth quadrants. Fisher’s exact test did not uncover a significant difference between the number of subjects with $\alpha < 1$ between SIT and STAND, nor between the Low and High elevation conditions for either body posture. Similarly, Fisher’s exact test did not reveal significant differences for the number of subjects with $\gamma < 1$. Pearson’s product-moment correlation coefficient was computed to further evaluate the relationship between conditions based on α and γ . At both elevations, there were strong positive correlations between body postures for each parameter. For both the SIT and STAND conditions, there were moderate positive correlations between elevations for α ; for SIT there was a weak negative correlation between elevations for γ , and for STAND there was a weak positive correlation between elevations for γ . Permutation tests did not reveal significant differences in either parameter between postures or elevations.

Table 5.1. Median CPT parameter fits

	α	γ	k
SIT Low	0.52 [0.20, 1.38]	0.91 [0.39, 1.22]	8.37 [0, 12.08]
STAND Low	0.68 [0.28, 1.23]	0.90 [0.52, 1.24]	6.88 [1.52, 18.21]
SIT High	0.67 [0.20, 1.51]	0.79 [0.62, 1.07]	6.75 [0.90, 21.01]
STAND High	0.37 [0.25, 1.40]	0.72 [0.45, 1.34]	9.74 [2.59, 29.39]

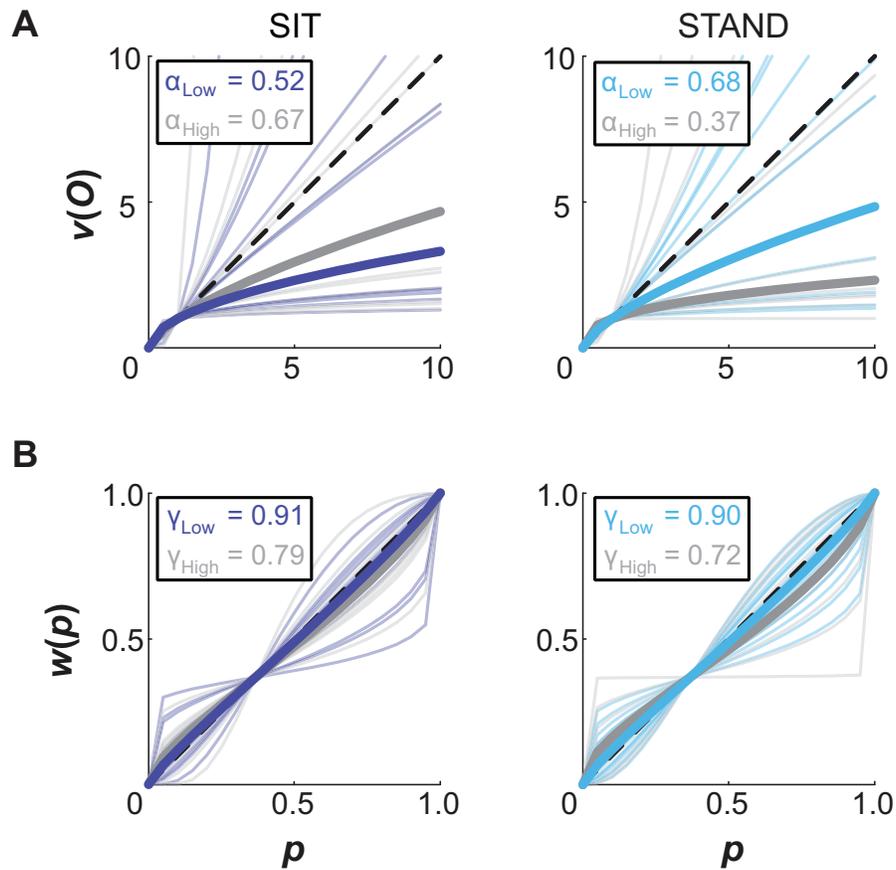


Figure 5.4. CPT curves. Cumulative prospect theory (CPT) model fits for (A) utility and (B) probability weighting in the SIT and STAND conditions. Thick lines indicate the median curves for Low elevation (colored) and High elevation (gray); thin lines correspond to fits for individual subjects.

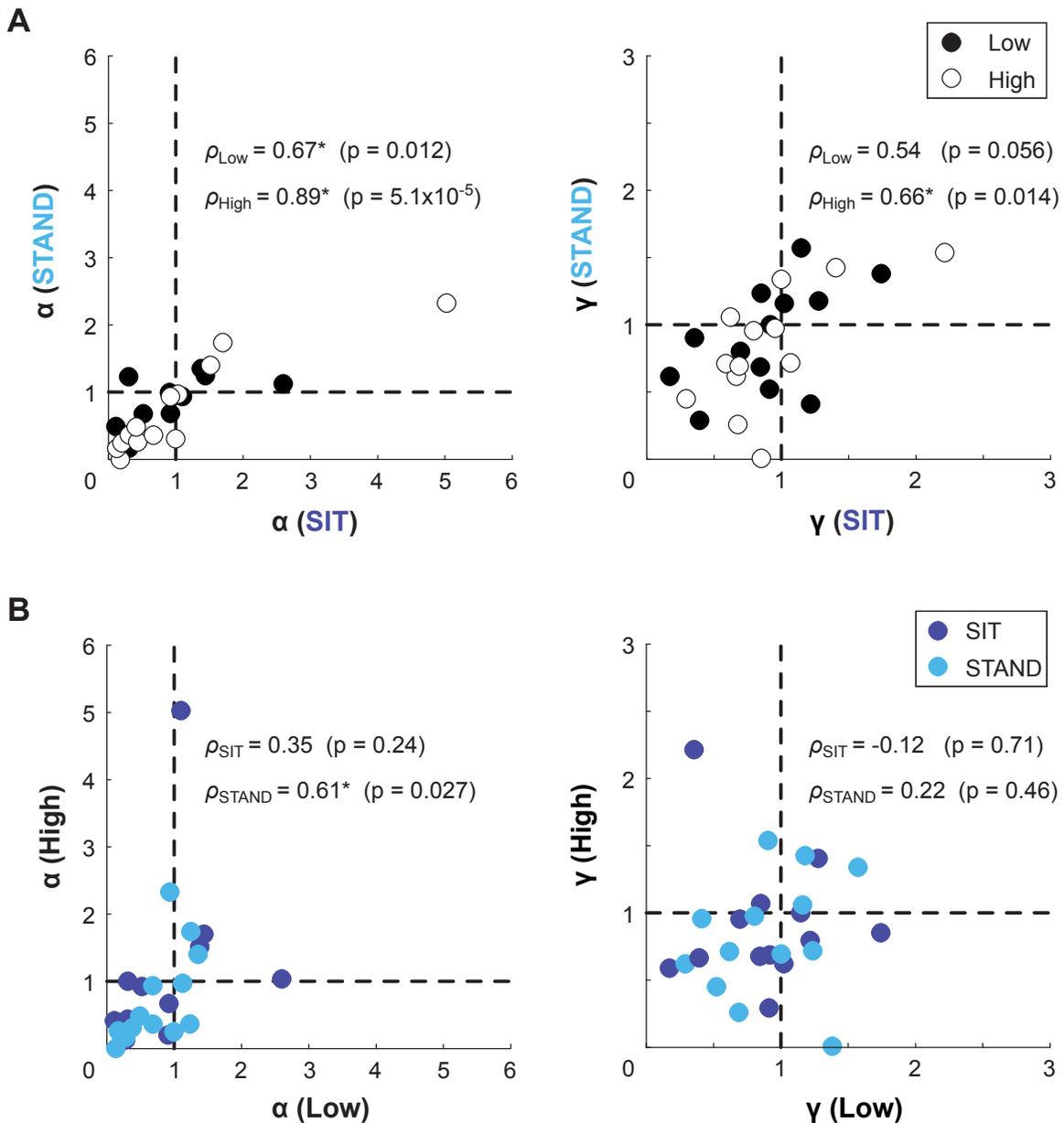


Figure 5.5. Individual CPT fits. Individual α and γ fits compared between conditions, including (A) body posture (SIT vs. STAND) and (B) elevation (Low vs. High). Risk preferences in utility were fairly consistent between conditions, as indicated by most α values lying within in the first and third quadrants of the plot. Probability weighting appears more idiosyncratic, with an increased number of values located in the second and fourth quadrants for γ .

5.4 Conclusions and Discussion

This is the first study to examine the effect of posture or postural threat on economic decision making. In this experiment, we compared risk-sensitivity between four conditions, including manipulations of body posture (sitting vs. standing) and threat (low elevation vs. high elevation). We recorded subjects' choices in a series of two-alternative economic lotteries, and we fit these choices to a model based on cumulative prospect theory. Neither altered body posture nor increased postural threat affected risk-sensitivity. Skin conductance, a measure of physiological arousal, did not change with body posture but did increase with elevation, confirming that the protocol was sensitive enough to discriminate between conditions. We conclude that economic choices possess a degree of robustness relative to emotional state, remaining relatively consistent in the presence of modest postural threat.

Ultimately, the postures and postural threat presented in this experiment did not affect economic decision making in healthy young adults. Our findings indicate that neutral postures such as sitting and standing are inconsequential to an unrelated economic task, and risk-sensitivity in an economic domain is less sensitive to emotional state than in the motor domain.

Previous studies have used similar lottery paradigms to investigate risk-sensitivity in economic tasks. Wu et al. (2009; 2011) analyzed subject choices across economic lotteries and equivalent motor lotteries for a rapid pointing task. Their resulting median parameters for the economic task align with our findings,

suggesting risk-aversion in utility and underweighting of large probabilities. Jarvstad et al. (2013) found comparable trends in utility and probability weighting for an economic lottery series using best fits from eight parameterizations of the CPT model.

We expected that subjects would become more risk-averse with more difficult postures and with increased postural threat. The different conditions presented in this experiment – standing compared to sitting and atop the 0.8m platform compared to ground level – are intended to elicit feelings of discomfort, instability, and fear of falling. Elevation in particular has a notable affect on psycho-social measures. Anxiety and fear of falling increase at the edge of a real or virtual elevated platform, while perceived confidence and stability decrease (Adkin et al., 2002; Cleworth, Horslen & Carpenter, 2012). These state changes are thought to induce altered performance in motor control tasks at increased surface heights due to the selection of a cautious strategy by the CNS. Specifically, individuals adopt a stiffening strategy and exhibit a limited range of motion at the edge of an elevated platform compared to ground level. Carpenter et al. (2001) showed this was true at a height of 0.81m, which is approximately the same height as the elevation threat presented in our experiment. We reasoned that a cautious policy, resulting from emotional feelings of threat and manifesting itself in the motor domain (which is highly salient to postural threat due to the potential for a fall), could also influence risk-sensitivity in an unrelated economic task.

Concerning our examination of postures, we have described that standing is less comfortable, more unstable, and more cognitively loading than sitting. Cognitive loading has been shown to alter risk preferences, as Whitney, Rinehart & Hinson (2008) demonstrated in a dual-task study of working memory and economic decisions under risk. When asked to memorize a string of alphabetic letters prior to choosing between a sure gain or loss and a gamble, subjects chose the gamble less often than when they did not receive a prior cognitive loading. This behavior was attributed to subjects choosing the computationally simple option due to a limited ability to process risk under the cognitive load. In our experiment, such behavior would lead to more risk-averse tendencies under the additional cognitive load of standing compared to sitting. Alternatively, it has been shown that we are more likely to choose options that have higher affective impact when cognitive resources are engaged in other tasks (Shiv & Fedorikhin, 1999). This suggests that high-reward lotteries would be favored more during a task with higher cognitive load, which would lead to more risk-seeking tendencies during standing compared to sitting. Our findings were inconsistent with either of the above reasonings, as risk preferences definitively did not change between sitting and standing. Indeed, the increased cognitive load during standing may not be large enough to trigger significant changes in risk-sensitivity. The additional attention required during standing does not necessarily deplete cognitive processes required for higher-level decisions. For example, in a study of potential effects of workplace posture for airport security screeners, there was no difference in screening performance

between sitting and standing (Drury et al., 2008). Similar risk preferences between sitting and standing substantiate the idea that risk-sensitivity in a movement domain, as in O'Brien & Ahmed (2013), is indeed a result of the actual movements and not simply due to the postures assumed during testing.

Actions have previously been shown to alter our perceptions (Witt & Brockmole, 2012). In our experiment, any action-related implications of a standing posture or increased elevation did not appear to affect perceptions of risk, either in utility or interpretations of probability. Despite feeling more threatened at a high elevation, as seen in skin conductance measures, our subjects' choices did not reflect an altered perceptions of the lottery risks. It is possible, however, that our elevated platform was not high enough to influence risk preferences. Other studies of elevation continue to see large changes in motor behavior at heights greater than 1.5m (Adkin et al., 2000; Adkin et al., 2002; Adkin et al., 2008; Davis et al., 2009; Cleworth, Horslen & Carpenter, 2012). Although elevations of ~0.8m do induce cautious motor strategies, conjunctive effects in an economic task may be muted at such a height, perhaps because the threat is less salient to this task. Although the platform height in this experiment was constrained by our laboratory ceiling, we are pursuing alternative techniques to increase perceived threat.

CHAPTER 6

LOSS AVERSION IN MOVEMENT EFFORT

6.1 Abstract

Our decisions are often swayed by a desire to avoid losses over a desire to acquire gains. While loss aversion has been confirmed for decisions about money or commodities, it is unclear how individuals generally value gains relative to losses in a movement domain. Current models of sensorimotor control assume that effort costs are minimized in the selection of movement strategies; however, if potential decreases in effort are valued differently than potential increases in effort, these models may offer an incomplete representation of movement decisions. We examined loss aversion in effort-based decision making, where decreased effort was framed as a gain and increased effort was framed as a loss. Subjects performed reaching movements with a robotic manipulandum against a viscous force-field, which could offer different levels of resistance (effort) against the reaches. They then chose to accept or reject different lotteries, each with possibility of performing a less effortful condition and a possibility of performing a more effortful condition, against the certain outcome of performing a medium level of effort. We used maximum likelihood estimation to fit subject-specific loss-aversion coefficients, λ , to

their choices. Subjects were loss-averse in the effort-based task ($\lambda_{\text{EFF}} = 1.26 \pm 0.09$), while they were significantly more loss-averse in an equivalent financial task ($\lambda_{\text{FIN}} = 2.52 \pm 0.31$). Our findings demonstrate that gains and losses in effort are not valued symmetrically, even in a simple arm-reaching movement.

6.2 Introduction

Empirical studies have directly confirmed that effort influences movement behavior. People tend to select low-effort movement strategies, such as exploiting motor redundancy in unfamiliar tasks (Ranganathan et al 2013), or walking along paths that require the fewest number of steps (Bitgood and Dukes 2005). Increasing effort can reduce frequency of changes of mind during goal-directed movement, suggesting that the criteria to correct initiated movements are dependent on energetic costs (Burk et al. 2014). Adding a distal load to the arm during free-stroke drawing results in altered movement strategies that minimize muscle effort (Wang and Dounskaia 2012). Effort minimization and motor learning also appear to be linked, as there is a distinct reduction in metabolic power during the learning of novel arm reaching dynamics (Huang et al. 2012).

However, some studies refute the contribution of effort on motor actions. Kistemaker et al. (2010) tested whether arm-reaching movements would adapt to expend less energy. The authors designed a novel force field, so that minimal energy trajectories deviated appreciably from trajectories in a null field. After practicing reaches along the minimal energy path, subjects did not alter their movements from those performed in the null field, thereby using more energy than needed to complete the task. One interpretation of this experiment is that minimization of effort is not an important factor in determining movement behavior. On the other hand, the central nervous system (CNS) may possess a more complicated representation of effort costs that contribute to these seemingly paradoxical findings.

A growing body of research considers motor control as a decision-making process under risk, where movement plans are chosen based on their ability to maximize rewards and minimize costs (Wolpert and Landy 2012). Current sensorimotor models often assume that the CNS is minimizing the sum of squared motor commands, which can be interpreted as an effort cost. Models incorporating an effort cost have successfully reproduced movement patterns during gait and arm-reaching (Nelson 1983; Alexander 1997; Uno et al. 1989; Kuo 2001; Todorov and

Jordan 2002; Emken et al. 2007; Izawa et al. 2008; Shadmehr et al. 2010; Berret et al. 2011). But other work suggests these cost functions do not fully capture individuals' internal representations and perceptions of effort, and thus they may be limited in describing movement behavior. For example, Körding et al. (2004) fit indifference curves for subjects experiencing different force magnitudes and durations, thereby inferring the form of effort cost rather than assuming it. They found a nonlinear relationship between these force components, which could not be modeled using a simple cost function but was highly conserved across subjects. Effort can also discount rewards (Prevost et al. 2010; Hartmann et al. 2013), providing further evidence that subjective valuation may play an important role in effort-based decisions. Additionally, clinical populations may have greater distortions in effort valuation compared with healthy individuals, such as in Parkinson's disease (Mazzoni et al. 2007).

Neuroeconomics provide a mathematical framework to assess movement behavior through economic and decision-making models. We have previously applied neuroeconomic principles to explore the utility function in an effort-based movement task. Using metabolic cost as an objective effort measurement, we observed distorted valuations of effort for subjects reaching against a viscous force

field (Summerside et al. 2014). Another well-established phenomenon in decision-making research is the phenomenon known as loss aversion. Our desire to avoid negative outcomes (losses) often surpasses our desire to acquire positive outcomes (gains), notably affecting our financial and commodity-based decisions (Tversky and Kahneman 1991). For instance, most people would firmly reject a lottery with a 50:50 chance of winning \$100 and losing \$100. A rational decision maker, however, would have no preference between playing the lottery (with an expected value of \$0) and refusing to play it (which would also have an expected value of \$0). Because losses loom larger than gains, people would not choose to play out this lottery until the gain is large enough to offset the pain of a potential loss. This means that the utility function is steeper for losses than for gains by a factor of approximately 2-2.5 (Kahneman et al. 1991; Tversky and Kahneman 1992).

Probing further into the subjective valuation of effort in movement, it is unclear how individuals might assess potential decreases in effort relative to increases in effort, and whether effort-based outcomes are valued symmetrically. If overall energy expenditure is a movement cost, we might consider reductions in effort as gains in a neuroeconomic framework, whereas additions in effort would be cast as losses. Would loss aversion manifest itself in this construction of effort-based

decision making? We tested the hypothesis that healthy young adults exhibit loss aversion in an effortful reaching movement, meaning that increases in effort are more undesirable than decreases in effort are desirable. We expected that loss aversion in effort would have a similar magnitude to that seen in classic financial tasks (wherein losses loom 2-2.5 times larger than gains).

6.3 Materials and Methods

Ethics statement

All subjects provided written informed consent before participation. The experimental protocol (14-0186) was approved by the Institutional Review Board of the University of Colorado Boulder in accordance with federal regulations, university policies, and ethical standards regarding human subject research.

Experimental protocol

During a preliminary training session, seated subjects (N=20, 12F/8M, 23.9 ± 4.0 yrs) made horizontal planar reaching movements using a robotic handle

(Interactive Motion Technologies Shoulder-Elbow Robot 2) while secured by a 4-point seatbelt (Fig. 6.1A). Optical encoders sampled the position of the robot handle at 200 Hz. The position of the handle controlled a cursor (0.4 cm radius) on a computer screen in front of the subject. A single trial required the subject to move the cursor from a home circle (0.7 cm radius) to a large rectangular target (15 cm wide, 4.3 cm high). The inside edge of the target was located 20 cm away from the center of the home circle. The home circle and target switched positions on every trial, so odd-numbered trials required reaches away from the body and even-numbered trials required reaches toward the body. Visual feedback encouraged subjects to complete the movement within 550 – 650 ms.

We manipulated the level of effort encountered during reaching by altering the damping coefficient \mathbf{b} in a viscous force field:

$$[F_x, F_y] = -\mathbf{b}[v_x, v_y]. \quad (6.1)$$

This viscous field produced a resistive force F , opposing the direction of movement and proportional to the handle velocity v . Subjects first performed 100 reaches at an intermediate level of effort ($\mathbf{b} = 35 \text{ N}\cdot\text{s}/\text{m}$), termed the “reference” resistance. They then trained at 10 conditions in a randomized order, including \mathbf{b} values below (0, 7, 14, 21, 28 $\text{N}\cdot\text{s}/\text{m}$) and above (42, 49, 56, 63, 70 $\text{N}\cdot\text{s}/\text{m}$) the reference. While reaching, they were shown a quantitative level of effort to describe to the condition as a percentage of effort relative to the reference, mapped onto \mathbf{b} values that were below (100, 80, 60, 40, 20% less) and above (20, 40, 60, 80, 100% more) the reference

(which in turn was designated as 0% less and 0% more). For each training condition, they performed 40 trials at a given resistance, followed by a 30-second rest and 20 additional trials at the reference resistance.

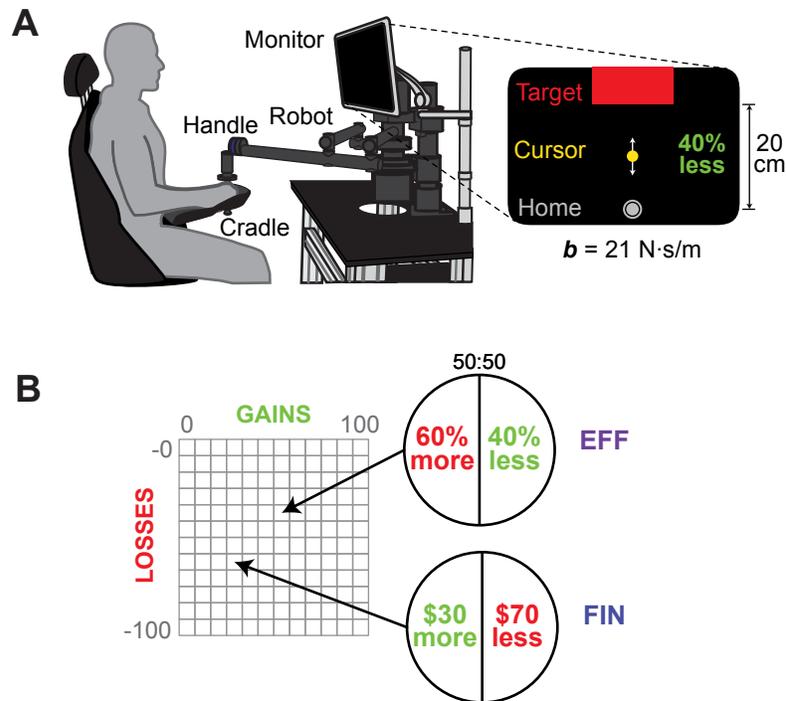


Figure 6.1. Experimental setup. (A) Subjects were trained in planar reaching movements using a robotic arm. Different levels of effort were presented by means of a viscous force field and designated as percentages more or less than the intermediate “reference” effort. (B) During testing, subjects were shown 50:50 gain-loss lotteries with more or less effort (EFF task) and with more or less money (FIN task).

In the testing session, completed immediately after training, subjects were shown a series of effort-based lotteries. Each lottery consisted of a 50% chance of having to reach against a higher amount of effort (above the reference, framed as a loss) and a 50% chance of having to reach against a lower level of effort (below the

reference, framed as a gain). Effort lotteries were constructed across gain and loss increments of 10% (EFF, Fig. 6.1B). Each lottery was shown three times, and the order of lotteries was randomized for each subject. Subjects indicated whether they would accept or reject each lottery using a handheld remote. After choosing to accept or reject a given lottery, they indicated whether this was a strong or weak preference. Prior to testing, subjects were informed that a random lottery would be selected and “played” at the end of the experiment. While playing out a lottery, subjects performed approximately 10 minutes of reaching movements (500 trials), with the same setup that was implemented during training. If the selected lottery had been rejected, the subject performed these reaches at the reference resistance; if the selected lottery had been accepted, a coin flip determined whether the subject performed these reaches at the higher or lower resistance.

In a separate, second testing session, 18 of the original participants repeated the effort lotteries (EFF2) and completed an analogous lottery task for financial decisions (FIN, Fig. 6.1B). The effort lotteries were always repeated before undertaking the financial lotteries. During this second session, subjects first performed a truncated version of training, which included a reminder of the reference resistance (80 trials), and four conditions in a randomized order (20 trials each, followed by 10 reference): 100% less, one of the resistances between 100% less and 0% less, one of the resistance between 0% more and 100% more, and 100% more. For the financial task, we endowed these subjects with \$30 cash at the end of the first testing session and scheduled their second session approximately one week

later. The subjects then brought \$60 cash to the second testing session, similar to the procedures presented in Tom et al. (2007). As with the effort task, one of the financial lotteries was selected and played at the end of the experiment. If the selected lottery had been rejected, the subject left with the original \$60 amount; if the selected lottery had been accepted, a coin flip determined whether the subject won additional money or lost money from the \$60 amount. Subjects were told to treat each financial lottery as though it would be played, but we did not select trials to play from lotteries that could result in them gaining or losing more than \$30.

Quantifying loss aversion

We quantified loss aversion by fitting subject responses to a model of choice based on prospect theory. Our previous findings indicate that there is only slight exponential valuation of effort-based utility (Ahmed et al. 2014). Thus, we assumed a linear utility function ($SV = X$, for $X > 0$; $SV = \lambda X$ for $X < 0$), where the loss-aversion coefficient, λ , describes how losses are valued relative to gains.

Maximum likelihood estimation was used to estimate subject-specific loss-aversion coefficients. The total utility of the presented lottery, with gain X^+ and loss X^- , is:

$$U_{\text{Lot}} = 0.5X^+ - 0.5\lambda(-X^-) \tag{6.2}$$

To compute the probability of accepting a given lottery, we used a logistic choice function with constant noise:

$$P_{\text{Lot}} = \frac{1}{1 + \exp[-kU_{\text{Lot}}]}, \quad (6.3)$$

where k is a parameter that accounts for stochasticity in a subject's choices, so $k=0$ characterizes random choice. Let r_i be the subject's choice on the i th trial, with $r_i = 1$ denoting acceptance of the lottery and $r_i = 0$ denoting rejection of the lottery in favor of reaching against the reference resistance. The estimated parameters (λ, k) maximize the likelihood function over n trials:

$$L(\lambda, k) = \prod_{i=1}^n P_{\text{Lot}}^{r_i} (1 - P_{\text{Lot}})^{1-r_i}, \quad (6.4)$$

We directly compared values of λ between the effort and financial choice tasks. A coefficient > 1 represents loss aversion, where losses (increases in effort) loom larger than gains (reductions in effort). A coefficient of 1 represents loss-neutrality, where gains and losses are valued equally. A coefficient < 1 represents gain-seeking behavior, where gains are more desirable than a loss is undesirable. In effort, we designate these behaviors as effort-averse, effort-neutral, and relief-seeking, respectively. Figure 6.2 illustrates possible loss-aversion coefficients for each of these cases and representative simulations of gain-loss decision matrices.

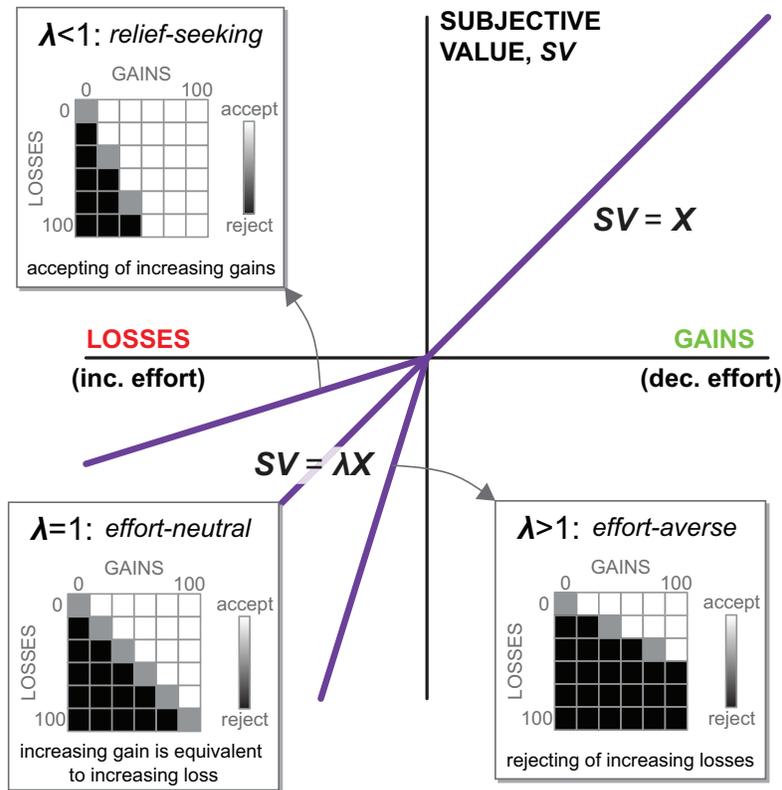


Figure 6.2. Defining loss aversion in effort-based utility. The loss aversion coefficient λ describes how an individual values losses (increases in effort) relative to gains (decreases in effort). This coefficient is fit from subject choices, portrayed in the corresponding gain-loss decision matrices. Effort-aversion corresponds to the typical loss aversion seen in finances and commodities, where losses loom larger than gains. In the effort domain, values of gains and losses range from 0 to 100 and are given as percentage-more or percentage-less resistance, respectively, relative to the reference resistance.

Ratings of Perceived Exertion

We also asked participants to rate their perceived exertion for different resistances to ascertain how their perception of effort scaled with viscous force and whether the changes in effort we presented were discernible to them. Prior to the training session, subjects performed reaches for the aforementioned training conditions without receiving feedback about the levels of effort. Instead, subjects

themselves evaluated the amount of effort required to complete a movement using Borg's Rating of Perceived Exertion (RPE) scale (Borg 1982). For each condition, they performed 50 trials at a given resistance, followed by a 30-second rest during which they gave the RPE for that resistance and 20 subsequent washout trials with no resistance.

Subjects also filled out an exit questionnaire in which they ranked the training conditions (from 100% less effort to 100% more effort) in order of their preferences if they had to perform 10 minutes of reaching against some resistance. The purpose of this questionnaire was to ensure that participants indeed perceived increasing effort as a loss. We excluded any subjects from our study if (1) they indicated a reversal of this preference on the questionnaire, or (2) they did not demonstrate the expected monotonic trends in lottery rejection (increased rejection of increasing losses and decreased rejection of increasing gains). Two additional subjects were tested who exhibited such behavior and have not been included in our analysis.

Statistics

We used the Mann-Kendall test to appraise monotonicity of the mean frequency of lottery rejection across task gains and losses. We used paired t-tests to examine differences in frequency of lottery rejection between the EFF and FIN tasks across gains and losses. We also used paired t-tests to make subject-specific comparisons of λ between tasks. We fit linear regression models to RPE as a

function of damping coefficient, as well as to λ_{EFF2} as a function of λ_{EFF} to characterize the repeatability of effort-based loss-aversion coefficients. For all statistical tests, the significance level was set to 5%.

We compared our loss-aversion model (with λ and k as free parameters) to a loss-neutral model (setting $\lambda=1$ and k as a free parameter) and a loss-aversion model with random choices. We quantified the quality of these models and their resulting parameter fits using the Akaike information criterion (AIC).

6.4 Results

Perceived exertion scaled linearly with resistance

Average ratings of perceived exertion increased with resistance (Fig. 6.3). Linear regression ($R^2 = 0.97$, $F = 283.73$, $p < 1 \times 10^{-7}$) verifies that subjects perceived linear increases in effort throughout the range of resistances tested, and they could differentiate between relatively small changes in the viscous field.

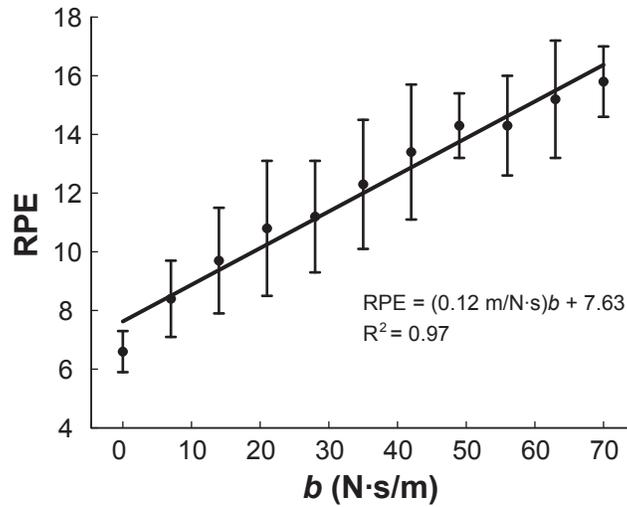


Figure 6.3. RPEs. Mean and standard deviation of RPE as a function of damping coefficient b in the viscous field.

Subjects are loss-averse toward effort, and more loss-averse toward money

In both EFF, rejection rates for all subjects decreased monotonically with increasing gains ($p < 0.03$) and increased with increased losses ($p < 0.004$), confirming that subjects valued increases in effort as aversive and reductions in effort as desirable (Fig. 6.4). Lotteries were rejected more frequently in the FIN task for all gains and for losses between 10 and 80 ($p < 0.04$).

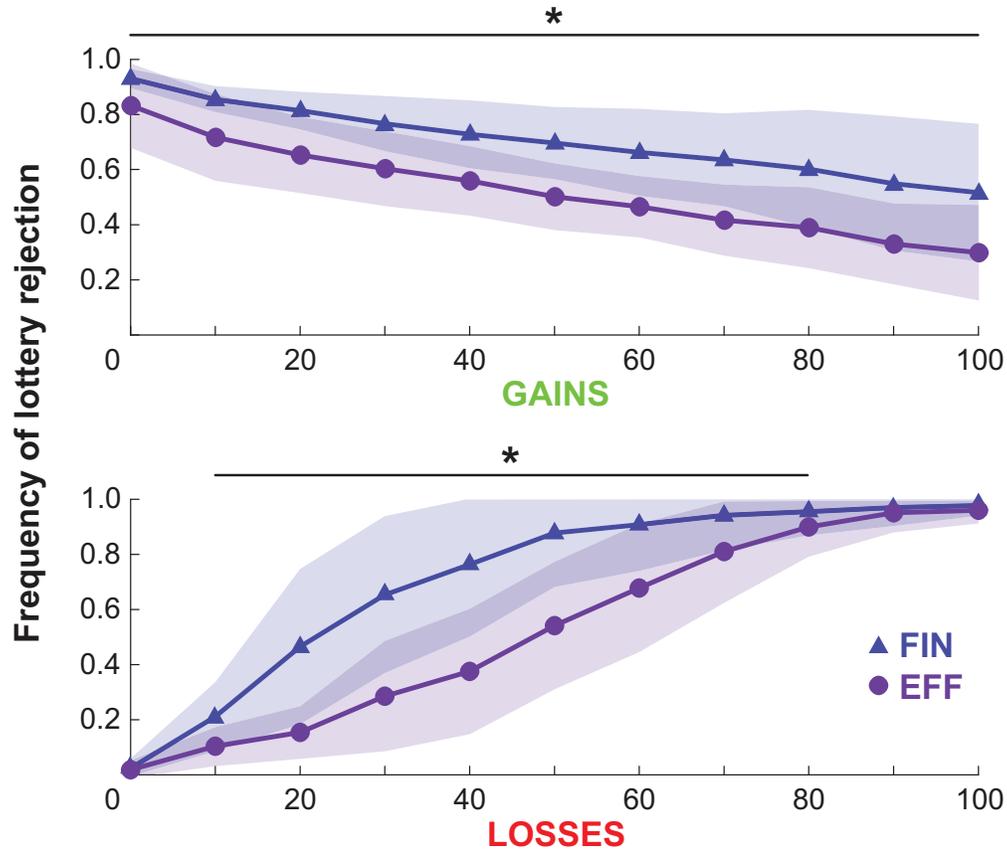


Figure 6.4. Frequency of rejecting lotteries. Mean and standard deviation of lottery rejection illustrates that the frequency of rejection decreases with larger gains and increases with larger losses. Asterisks (*) span across gain/loss values for which there is a significant different between the FIN and EFF task ($p < 0.05$).

Example decision matrices and loss-aversion coefficients for a representative subject in each task are shown in Fig. 6.5, directly illustrating a higher rejection rate for the financial lotteries. For the EFF task, our model predicts subjects' average probability of rejecting a lottery at 56.4%, and, in actuality, subjects rejected 52.4% of the lotteries shown. For the FIN task, our model predicts an average probability of rejection at 71.2%, and subjects had an actual rejection rate of 70.4%.

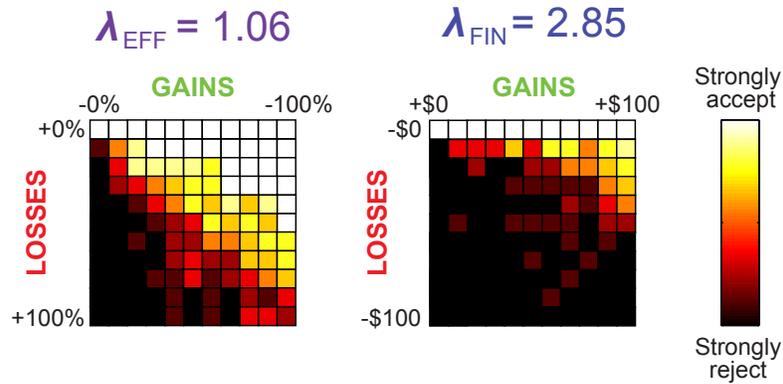


Figure 6.5. Example decision matrices. Frequency of accepting and rejecting lotteries across gains and losses for an effort task (left) and an equivalent financial task (right).

From our model, mean (\pm SEM) λ parameter fits demonstrate that subjects were loss-averse in effort, with $\lambda_{\text{EFF}} = 1.26 (\pm 0.09)$, and this value is significantly larger than 1.0 ($p=0.006$). On average, subjects were twice as loss-averse in the financial task, with $\lambda_{\text{FIN}} = 2.52 (\pm 0.31)$ ($p<0.001$). These relative distortions between gains and losses are illustrated in Fig. 6.6, and individual subject values are compared between the two tasks in Fig. 6.7. Mean (\pm SEM) k parameter fits for both tasks were $k_{\text{EFF}} = 0.18 (\pm 0.02)$ and $k_{\text{FIN}} = 0.49 (\pm 0.24)$.

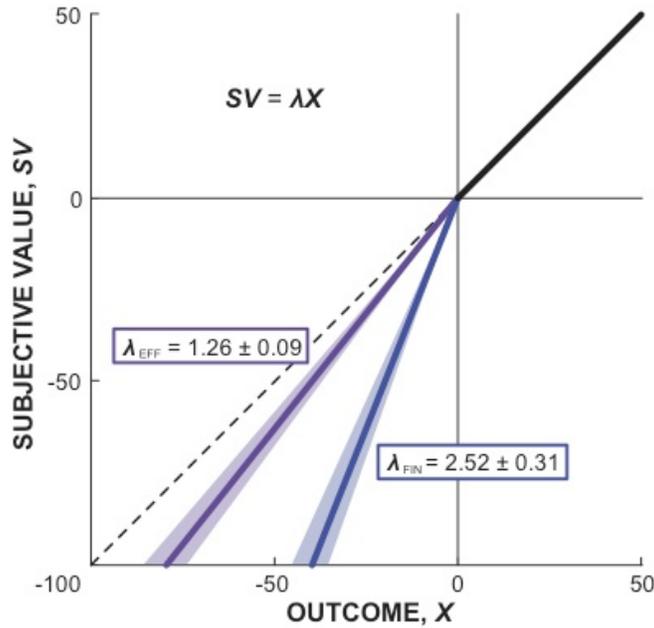


Figure 6.6. Loss-aversion coefficients. Subjects exhibited loss aversion in both EFF and FIN tasks. Mean and SEM loss-aversion coefficients suggest that increasing effort is more undesirable than decreasing effort is desirable. The effect is not as strong as in a financial context, where subjects' dislike of losing money was more than twice the appeal of gaining money.

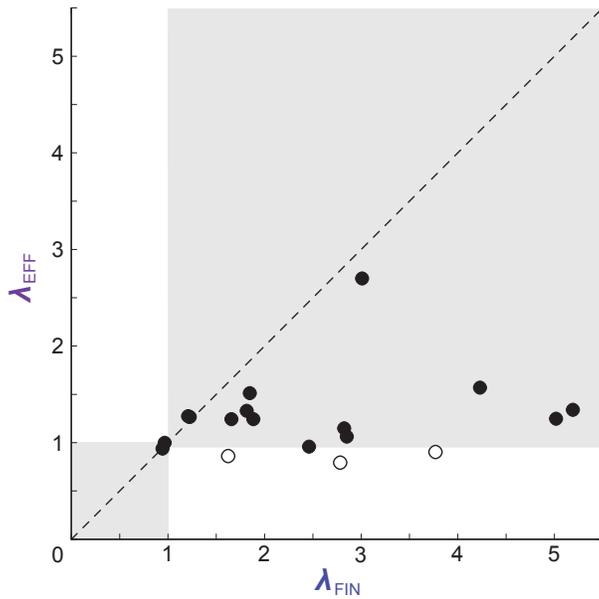


Figure 6.7. Comparison between EFF and FIN coefficients for each subject. Closed circles (points in the shaded region) indicate similar directionality in λ between the two tasks, whereas open circles indicate opposing directionality in λ .

Loss aversion in effort is repeatable

Of the 18 subjects who participated in the second testing session (in which they repeated the effort lotteries), 16 showed consistent directionality in loss-aversion coefficients. That is, most subjects were either relief-seeking in both sessions (4 subjects) or effort-averse in both sessions (12 subjects). A comparison of λ_{EFF} and λ_{EFF2} values is given in Figure 6.8. The majority of data points lie above the unity line, illustrating that λ_{EFF2} is consistently larger than λ_{EFF} , and a regression analysis confirms that the relationship between coefficients from the first and second sessions is fairly linear ($R^2 = 0.66$, $F = 29.59$, $p < 1 \times 10^{-4}$). The mean (\pm SEM) loss-aversion coefficient from the repeated effort task was $\lambda_{\text{EFF2}} = 1.50$ (± 0.13). Paired t-tests reveal that these second-session coefficients are significantly different from λ_{EFF} ($p = 0.002$) and from λ_{FIN} ($p = 0.005$).

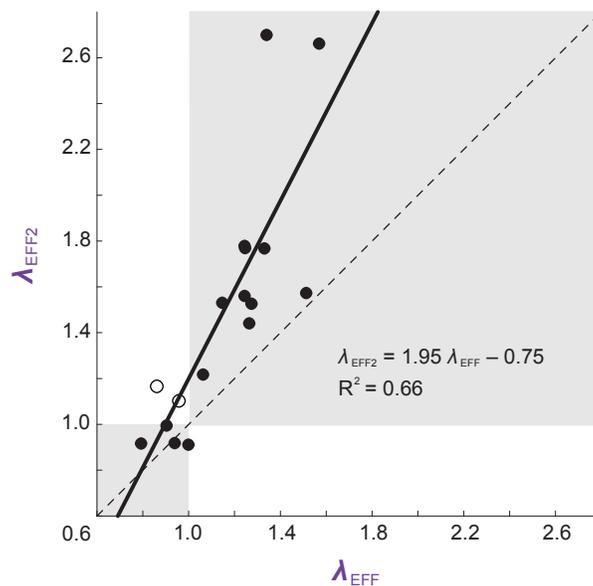


Figure 6.8. Comparison between EFF and EFF2 coefficients for each subject. Closed circles (points in the shaded region) indicate similar directionality in λ between the two tasks, whereas open circles indicate opposing directionality in λ . Nearly all subjects were more loss-averse on the second day of testing.

Model comparisons

For both the EFF and FIN tasks, our model incorporating the loss-aversion coefficient (mean AIC: 191.9 EFF, 92.3 FIN) performs better than a model with $\lambda = 1$ (mean AIC: 247.9 EFF, 314.6 FIN) or than random-choice (mean AIC: 520.1 EFF, 512.8 FIN). Fitting an exponential distortion in the utility function did not improve the likelihoods of our parameter fits.

6.5 Conclusions and Discussion

This is the first study to examine how increases in effort (losses) are subjectively valued relative to decreases in effort (gains). Subjects were trained to perform reaching movements against different levels of resistance, and they chose to accept or reject related effort-based lotteries. We found that the effort utility function is steeper for losses than for gains by a factor of 1.26, and this factor was fairly consistent across subjects. In an equivalent financial task, the same subjects valued losses more strongly than gains by a larger average factor of 2.52, which agrees with previous findings of loss aversion in the economic domain (Kahneman et al. 1991; Tversky and Kahneman 1992).

In their formulation of prospect theory, Kahneman and Tversky (1979) introduce the reference-dependent property of loss aversion, wherein gains and losses are all measured relative to a reference point. The authors note that the formulation of risky prospects and the expectations of the decision maker can affect

the location of this reference. Current models of sensorimotor control often incorporate effort as a cost to be minimized but do not account for the possible existence of a reference point. Importantly in our study, subjects would always have to exert some amount of effort regardless of their lottery decisions, imparted through the 10 minutes of reaching performed at the end of the experiment. An implicit assumption of these models is that some amount of effort must be exerted, and an optimal movement minimizes those effort costs. We established a reference point in the form of an intermediate level of resistance (0% more effort, and 0% less effort). Effort-based gains and losses were presented as decreases and increases from the reference. We have thusly demonstrated that a reference point in effort can be externally imposed, confirming that prospect formulation can affect its location. The reference point may change for different arrangements of risky choices and for other movement tasks.

Our findings may explain behavioral studies in which individuals do not appear to prioritize effort minimization. For instance, Kistemaker et al. (2010) noted that subjects did not adopt reaching movements to follow a minimum-energy path, choosing instead to perform more effortful straight-line reaches. If increases in effort were valued more strongly than decreases in effort, subjects would not necessarily seek the lower effort paths. Because of the seemingly dynamic nature of the reference point in effort-based utility, the force field introduced in that experiment may have altered subjects' perceptions of a reference effort. Then, they would prefer avoiding more effortful movements (above that reference) to reducing

movement effort. This, in conjunction with other factors such as minimizing variance (Harris and Wolpert 1998), may account for the straight-line trajectories observed in such an environment.

An ensuing question is whether effort aversion depends on the magnitude of effort. Subjects' perceived exertion increased with viscous field resistance, but the amount of effort encountered in this task was fairly modest; reaching against even the largest resistance was not exceptionally taxing. Would we see the same amount of effort aversion for larger amounts of effort? In the financial domain, there is conflicting evidence regarding the extension of loss aversion to different amounts of money. Increasing availability of free-spending income has been shown to attenuate loss aversion (Wicker et al. 1995), but a recent socio-demographic study found instead that higher wealth and income are associated with stronger loss aversion (Gächter et al. 2010). A reversal of loss aversion has even been observed for small monetary outcomes (e.g. less than 1€), attributed to the hedonic principle and cognitive discounting (Harinck et al. 2007). Loss aversion has been shown to increase for larger financial outcomes (Wicker et al. 1995; Ert and Erev 2013), and this magnitude effect could feasibly hold for effort aversion.

It may, in fact, be difficult to extend the risky-choice lottery paradigm to more naturalistically effortful movements, as these movements could be construed as forms of exercise (i.e. walking, running, weight lifting, push-ups, pull-ups). Consider an example: would you rather run one mile for sure, or have a 50:50 chance of running either half of a mile or two miles? There are many potentially

confounding factors that could affect one's motivation and choices in a laboratory setting. Are you a frequent runner? How would this run fit in with your exercise regimen, if one exists? Are you feeling physically well and energized? Did you eat a big breakfast and want to work it off? Did you eat a big breakfast and are now lethargic? Depending on a person's physical state and frame of mind at the time of the experiment, increased effort may not necessarily be considered a loss, and individuals may possess firm, preexisting reference points for certain movement tasks. Ironically, the possible variation in subjects' interpretations of effort-based gains and losses complicates empirical measurement of the subjective value of effort, but it also attests to the importance of accounting for subjective value of effort to explain movement decisions. The subjects included in our study expressed a preference for lower resistances over high resistances, confirming that they viewed increased effort as a loss in the context of this experiment. Alternative methods and controls may be required to tease out relative gain/loss valuation for higher levels of effort.

Effort aversion was repeatable, with subjects still valuing effort losses more strongly than gains approximately one week after the initial testing session. Interestingly, effort aversion was slightly but consistently more pronounced during the second testing session, with an average loss-aversion coefficient of 1.50 compared with the original 1.26. A possible explanation for the increased effort aversion lies in the difference between anticipating outcomes and experiencing outcomes. Experience with losses may attenuate loss aversion (Novemsky and

Kahneman 2005; Kermer et al. 2006) because repeated exposure to losses teaches people that the negative outcome is not as bad as they predicted. In our experiment, subjects undergo a lengthy training procedure prior to the initial testing session, experiencing 11 total resistances twice as they perform RPEs and effort feedback training. They receive considerably less training prior to a second testing session the following week, experiencing five total resistances with fewer trials than before. Reduced training on effort outcomes during the second day of testing may have elevated effort aversion, with subjects relying more on forecasting than direct experience. An alternative explanation is that the experience gathered when playing out a lottery at the end of the first session (requiring 10 minutes of arm-reaching against some resistance) actually increased effort aversion during the second session. Subjects may have been more sensitive to losses (increases in error) during the second session after having experienced the lottery play-out, and they accordingly rejected more high-loss lotteries.

Ultimately, the observed effort aversion in arm-reaching suggests that movement decisions are geared toward avoiding higher effort over acquiring lower effort. This finding has important implications for computational models of sensorimotor control. Presently, these models fail to account for subjective representations of effort that may factor into our movement decisions. Understanding subjective representations of effort will help us simulate and predict behavior for a wider range of movement decisions.

CHAPTER 7

THESIS CONCLUSIONS

I have presented four studies investigating decision-making preferences in movement under risk. Below, I summarize the major findings of these studies, discuss their implications, and suggest directions for future research.

7.1 Summary of Findings

1. Humans exhibit irrational behavior in goal-directed movements for external rewards and costs.

a. Individuals are more risk-seeking in whole-body leaning movements than in arm-reaching.

b. This finding is robust to experimental paradigm, manifesting itself through a continuous motor task as well as in discrete lottery decisions.

c. Manipulating risk (through outcome rewards and penalties, or through motor variability) and threat (when the threat is salient to the decision task) affects movement decisions so that they are more rational or more irrational.

- 2.** Irrationality in movement can arise from:
 - a.** Poor estimations of movement variability
 - b.** Distortions in the utility function
 - c.** Distortions in the probability weighting function

- 3.** Humans exhibit irrational behavior in decisions about internal movement costs.
 - a.** Individuals express loss aversion in effort, finding increases in effort to be more undesirable than decreases in effort are desirable.

- 4.** Risk preferences generalize between arm-reaching and whole-body leaning movements, with individuals demonstrating risk-seeking tendencies for both tasks.
 - a.** Greater underestimation of motor variability results in increased risk-seeking behavior in the whole-body movement.

- 5.** Postural threat affects risk-sensitivity in relevant decision tasks. Risk preferences in non-relevant tasks are robust to postural threat.
 - a.** Elevation increases irrationality in whole-body leaning, resulting in more risk-averse behavior due to overweighting small probabilities.
 - b.** Elevation does not affect risky decisions in arm-reaching.

c. Elevation does not affect risky decisions in the economic domain, and this finding holds for both sitting and standing body postures.

6. Humans exhibit loss-aversion in both economic and effort-based decisions.

a. This effect is stronger in an economic domain, as the desire to avoid financial losses is stronger than the desire to avoid moderate increases in effort.

7.2 Implications of Work

Movement is an essential component of our lives. Consciously or subconsciously, our brains are constantly making decisions about how to move our bodies through space, whether on a small scale (i.e. reaching for a cup of coffee) or on a large scale (i.e. driving to work). The empirical and computational methods presented in this thesis have contributed to our understanding of how individuals choose among different movement strategies, and how the environment or frame of mind affects such choices. Healthy young adults make irrational decisions in movement under risk, but manipulating risk (as seen in Chapter 3), threat (as seen in Chapter 4), and movement costs (as seen in Chapter 6) can alter their motor strategies and decision preferences. This finding has transformative consequences for behavioral, computational, and clinical research.

7.2.1 Behavioral implications

Characterizing and predicting movement behaviors remains an ongoing problem in motor control. Movement performance in one environment does not dictate biomechanical and psychological outcomes in settings with increased risk or threat. For example, an athlete successfully practicing difficult motor skills in a secure training environment does not necessarily tell us how she will perform outside of training or in competition. Due to the potentially damaging consequences of a poor decision, the ability to anticipate and train risky movement behavior is a cornerstone of injury prevention and treatment. I have begun answering the question of whether it is possible to predict behavior and alter risk preferences in movement. Concerning the ability to predict movement under risk, I have shown that risky behavior does generalize between dissimilar movements, and poor estimates of motor variability result in less rational behavior. In addition, threat appears to only affect movements that require direct confrontation with the threat, whereas preferences are unaffected if the threat is not salient to the decision task. Finally, individuals are keener to avoid increases in effort than to seek decreases in effort, which may provide insight into movement choices when there are competing options that would require different amounts of effort. I have also demonstrated that decision preferences in movement can be altered. Imposing explicit rewards and penalties to simulate moving toward a cliff revealed risk-seeking tendencies in both arm-reaching and whole-body leaning. However, increasing the penalty of “falling over the cliff” and increasing motor endpoint variability through added

noise both notably affected movement endpoints, which subjects staying further away from the cliff edge. Postural threat affected whole-body movement decisions, specifically distorting the probability weighting function and resulting in greater overweighting of small probabilities. Lastly, individuals are loss-averse in moderate effort relative to a reference. Enforcing a reference point in effort can influence valuation of gains and losses in effort, and adjusting this reference point may impact gain/loss asymmetry. Furthermore, understanding the subjective valuation of effort would enable the design of personal training programs (i.e. for exercise or rehabilitation), leveraging effort to adjust movement behavior.

7.2.2 Computational implications

Computational models of sensorimotor control often assume that the CNS selects movement strategies that will minimize some cost function. A number of cost functions have been proposed which can successfully replicate movement patterns in arm-reaching and gait. Some cost functions have been disputed or proven to have bounded applications (Flash and Hogan 1985; Uno et al. 1989), and it is unclear to what extent other cost functions may generalize to other movements, motor paradigms, and environments. To date, very few studies have incorporated risk-sensitivity (Whittle 1981; Nagengast et al. 2010; Medina et al. 2012a, 2012b; Grau-Moya et al. 2012) or subjective valuation of effort costs and rewards (Rigoux and Guigon 2012) into cost functions. This dissertation confirms that both risk-sensitivity and subjective valuation of outcomes play prominent roles in movement,

and future mathematical formulations must account for these factors to fully describe movement decisions.

7.2.3 Clinical implications

Subjective representations of the rewards, costs, and probabilities involved in movement may also be crucial to understanding motor behavior for older adults and clinical populations. Generally, older adults exhibit a limited range of motion, have a larger variability in their movement, and take more time to complete a motor task in comparison with a younger population (Pratt et al. 1994; Cooke et al. 1989). These altered movement patterns in older adults are usually attributed to biomechanical constraints (i.e. declines in various physiological systems that occur as we age, such as impaired muscle function). But movement is also a decision-making process. Perhaps cognitive and psychological factors (in addition to or rather than biomechanical factors) are also at play. Distortions in outcome utility, probability weighting, or motor variability estimation may also change with age, affecting risk-sensitivity and, in turn, contributing to these altered movement strategies.

Effort valuation also appears to explain certain motor behaviors. Striking evidence for this can be seen in Parkinson's disease (PD), a chronic movement disorder. PD affects 1-2% of the population and causing motor impairments such as bradykinesia (slowness of movement). PD arises from decreased production of the neurotransmitter dopamine in the brain. Previously, bradykinesia had been

thought to result from the speed-accuracy tradeoff; that is, PD patients slow their movements to compensate for a loss of accuracy at normal speeds. Mazzoni et al. (2007) tested instead whether bradykinesia is an implicit decision caused by a shift in the cost/benefit ratio of moving fast. In their study, subjects made 20 reaching movements toward targets at different distances and with different movement time requirements. PD subjects did not exhibit significantly different endpoint accuracy from control subjects, but they consistently needed more trials to make the 20 valid movements. PD subjects were reluctant to move quickly even though accuracy was not compromised, indicating that Parkinsonian patients have a higher probability of moving slowly because of a distortion in speed selection mechanisms, and movements with lower energy expenditure are favored. My work on loss aversion in effort-based movements suggests that we could employ economic principles to increase movement speeds for PD patients. For example, framing movement effort as gains and losses relative to a variable reference may be an effective means of recalibrating perceived energy expenditure, thereby shifting the cost/benefit ratio of faster movements in the opposite direction.

7.3 Future Directions

The research presented in this dissertation exposes irrational decision preferences in movement under risk. Future studies of motor behavior would be well suited to continue quantifying subjective rewards and costs in movement.

The first two studies revealed that risk-sensitivity in movement arises from poor estimations of motor variability, distorted valuation of external rewards/penalties, and distorted weighting of outcome probabilities. Despite its prevalence, risk-sensitive movement behavior is not steadily considered in optimal control models. Recently, Todorov et al. (2012) unveiled a physics engine for model-based control. This engine, named MuJoCo (which stands for Multi-Joint dynamics with Contact), introduces various improvements in speed, simulation accuracy, and contact dynamics. The end result is an optimization controller that can simulate behavior of multi-joint dynamical systems in a physically realistic manner. For example, the authors have used MuJoCo to model running, walking, and other complex behaviors of humanoids and quadrupeds in a three-dimensional environment. Presently, MuJoCo does not incorporate risk-sensitivity in its computation of optimal control schemes. Another natural extension of my research in risk-related behavior, then, would be to design a risk-sensitive cost function within MuJoCo to simulate optimal behavior for various multi-joint bodies in risky environments.

The fourth study warrants further exploration of the subjective value of effort in movement control and decision making. It remains to be seen whether effort-based loss aversion is present for more naturalistically effortful movements, such as walking or running. Moreover, incorporating subjective effort valuation into descriptive sensorimotor models may offer more robust predictions of movement behavior than normative models based on objective effort costs.

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