博　士　論　文（要約）

Risk-sensitive decision making in motor tasks with an asymmetric gain function

(非対称な利得関数を持つ運動課題におけるリスク感受的な意思決定)

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List of abbreviations

Chapter 1

Abbreviation	Term
EU	Expected utility
$EG(S)$	Expected gain for given a selected movement plan
$G(t\|w)$	Gain function of movement trajectory for given a state of world
$P(t\|S)$	Probability distribution of a movement trajectory for given a selected movement plan
$P(v\|w)$	Likelihood function which links sensory information to a state of world
$P(w)$	Prior distribution of a state of world
$P(w\|v)$	Posterior distribution of a state of world for given sensory information
S	Movement plan
$S = d(v)$	Decision function which maps from sensory information to a movement plan
t	Possible movement trajectory
U	Utility
v	Possible sensory information
w	Possible state of world

Chapter 2, 4, & 6

Abbreviation	Term
t	Executed response time
T	Planned response time
$EG(T)$	Expected gain for given planned response time
T_{obs}	Observed mean response time
T_{opt}	Optimal mean response time
$G(t)$	Gain function of executed response time

$P(t\|T)$	Probability distribution of executed response time for given planned response time

Chapter 3

Abbreviation	Term
$EG(P)$	Expected gain for given a planned ball stop position
$G(p)$	Gain function of a ball stop position
p	Observed ball stop position
P	Planned ball stop position
$P(p\|P)$	Probability distribution of an observed ball stop position for given a planned ball stop position

Chapter 3

Abbreviation	Term
e	Executed movement endpoint
E	Planned movement endpoint
$EG(E)$	Expected gain for given a planned movement endpoint
E_{obs}	Observed mean movement endpoint
E_{opt}	Optimal mean movement endpoint
$G(e)$	Gain function of an executed movement endpoint
$P(e\|E)$	Probability distribution of an executed movement endpoint for given a planned movement endpoint

Chapter 1.

Introduction

1-1. Significance of decision making in sports

In highly skilled movement, especially in sports, an appropriate decision-making is important for superior performance. For example, in tennis or table tennis, the closer to an edge of a line player aims for and a ball bounces inner side of the line, the more probabilities of scoring a point increase. However, the ball bounce of outer side of the line loses a point. In such situation, where player should aim for depends on his/her sensory motor variability. A skilled player who has small ball bounce variance should aim close to the line, while performance drops if a novice player aims for the same point as the skilled player since his/her large ball bounce variance leads to lose a point. Therefore, under the situation in which higher performance comes with risk of failure, the decision where player aim at crucially influences his/her performance. Nevertheless of the significance of decision-making in sports, it is unclear whether humans aim optimally under such asymmetric gain function in which higher gain comes with a risk of zero gain. Therefore, the present thesis aims to elucidate characteristics of decision-making in motor tasks with an asymmetric gain function.

In Chapter 1-2, I first review a short history of economic decision-making studies. In Chapter 1-3, I then review studies of motor decision-making and explain the mathematical framework that defines an optimal motor decision. Finally, I state the purpose of the present thesis in Chapter 1-4. In Chapter 1-5, I demonstrate a brief summary in each Chapter.

1-2. Irrationality of decision-making in economic and psychological tasks

A lot of economic and psychological studies have been conducted to understand the processes that lead to the rationality or irrationality of decision-making. The theory of decision-making goes back to the eighteenth century (Bernoulli, 1954/1738) and has developed into different models of decision-making (Bell, 1985; Kahneman & Tversky, 1979; Markowitz, 1952; Pratt, 1964; Savage, 1954; Von Neumann & Morgenstern, 1944). The theory of decision-making is roughly divided into two models: perspective theory of rational decision making (Bernoulli, 1954/1738; Savage, 1954; Von Neumann & Morgenstern, 1944/1953) that attempts to predict what a rational decision maker should choose and descriptive theory of irrational decision making (Bell, 1985; Kahneman & Tversky, 1979; Markowitz, 1952; Pratt, 1964; Simon, 1956) that attempts to capture what a human decision maker actually choose. In Chapter 1-2, I briefly review these two models and show that a human decision maker can behave irrationally in economic and psychological tasks.

1-2-1. Expected utility theory as a perspective theory of rational decision making

Expected utility theory is the perspective theory, first proposed by Bernoulli in 1738 (Bernoulli, 1954/1738), and developed by Von Neumann & Morgenstern (1944/1953) thereafter. Expected utility theory defines the expected utility of an action as $EU(a) = \sum P(o|a) \cdot U(o)$, where $P(o|a)$ is the probability that an action a leads to a positive outcome o and $U(o)$ is the utility of the outcome. The principle of maximum expected utility states that a rational decision maker should choose the action $a^* = a\underset{a}{\mathrm{rgmax}}\, EU(a)$ in order to maximize the expected utility. The utility indicates the subjective value of the positive or negative outcome and is not always equal to the objective value of the outcome.

For example, a decision maker is faced with the choice between two lotteries. One is a gambling lottery that has 50% chance of winning \$1,000 but 50% chance of winning nothing. The other is a sure lottery that has 100% chance of winning \$500. Even though the expected payoff of two lotteries is same but most people prefer to choose the sure lottery. In other words, the expected utility of 50% winning of \$1,000, $\frac{1}{2}U(\$1{,}000)$, is less than the expected utility of certain \$500, $U(\$500)$. To explain this behavior, Bernoulli (1954/1738) hypothesized that the utility of money follows a logarithmic law $U(\$x) = \log(x)$ so that it diminishes as an amount of money increases, is known as the law of diminishing marginal utility. The diminishing marginal utility is equivalent with risk-averse attitude. Risk-averse decision maker chooses a sure lottery even if it has a lower payoff, for example, \$420. This \$80 difference in expected payoff between two lotteries is called a risk-premium that risk-averse decision maker is prepared to pay \$80 to avoid risk (like purchasing insurance). In contrast, risk-seeking decision maker that has a belief of increasing marginal utility prefers a gambling lottery even if a sure lottery has a higher payoff of \$580 (like betting in a casino).

1-2-2. Violations of expected utility theory

Expected utility theory proposes the normative axioms of rational decision making. However, in actual human choice behavior, the violations of the normative axioms in expected utility theory has been repeatedly confirmed (Allais, 1953; Ellsberg, 1961; Slovic & Tversky, 1974). One of the most famous violations is the Allais paradox (Allais, 1953), where a decision maker is faced with two different decisions that essentially present the same choice, but shows an inconsistent preference reversal (Braun et al., 2011). Allais (1953) presented two problems. The first problem is to choose between lottery A (1.0, \$100) or lottery B (0.1, \$500; 0.89, \$100; 0.01, \$0). Lottery A means 100% chance to win \$100. Lottery B means 10% chance to win \$500, 89% chance to win \$100 and 1% chance to win nothing. The second problem is between lottery C (0.11, \$100; 0.89, \$0) or lottery D (0.1, \$500; 0.9, \$0). If we add a common consequence of 89% chance to win \$100 (0.89, \$100) to lottery C and D, lottery C and D becomes lottery A and B, respectively. Thus, these two problems are essentially the same. However, most people prefer lottery A in the first problem and prefer lottery D in the second problem. This preference is apparently inconsistent because the first preference is reversed in the second problem. This preference reversal violates the independent axiom underlying expected utility theory (Kahneman & Tversky, 1979).

Kahneman & Tversky (Kahneman & Tversky, 1984; Tversky & Kahneman, 1992) suggested the fourfold pattern of risk that decision maker's preferences violate expected utility theory, as described flowing. Individuals tend to be risk-averse for high probability gain (as in the first problem of the Allais paradox), whereas they tend to be risk-seeking for low probability gain (as in the second problem of the Allais paradox). However, when lotteries are framed in terms of loss rather than gain (for example, lottery A of the Allais paradox is 100% of losing $100 and lottery B is 10% of losing $500, 89% losing of $100, and 1% of losing nothing), risk preferences are reversed, called framing effect. Individuals tend to be risk-seeking for high probability loss (i.e., hoping not being incurred losses), whereas they tend to be risk-averse for low probability loss (as when purchasing overseas insurance).

1-2-3. Prospect theory as a descriptive theory for actual human behavior

To account for such human choice behavior that violates expected utility theory, Kahneman & Tversky (1979) proposed prospect theory, which is categorized as a descriptive theory of decision-making. Prospect theory states that decision process goes through two stages. In the first stage, decision maker edits offered prospects (i.e., lotteries) as gains or losses relative to a reference point, not as absolute gains or absolute losses. In the second stage, decision maker evaluates the offered prospects and chooses the highest subjective expected value of the prospect. The subjective expected value, $SEV = \sum_i^n w(p_i) \cdot v(o_i)$, is defined as sum of the product of weighted probabilities $w(p_i)$, which represents the subjective distortion of the objective probability p_i, and subjective values of outcomes $v(o_i)$, which represents the subjective gain or loss of the objective outcome o_i.

Kahneman & Tversky (Kahneman & Tversky, 1979; Tversky & Kahneman, 1992) could successfully account for human decision-making process by introducing the value (i.e., utility) function and the probability weighting function (Figure 1-1A&B). The S-shaped value function has a concave shape for gains, which indicates the diminishing marginally utility leads to risk-averse behavior and has a convex shape for losses, which indicates the increasing marginally utility leads to risk-seeking behavior. Furthermore, the slope for losses is steeper than that for gains (Figure 1-1A), known as loss aversion, which explains the Allais paradox. Most people prefer lottery A (1.0, $100 million) to lottery B (0.1, $500 million; 0.89, $100 million; 0.01, $0) because they edit outcomes of lottery B as gains and losses relative to a reference point. If we edit $100 million as a reference point, the subjective evaluation of $-$$100 million for losses (i.e., difference of $100 million and $0 million) is larger than the subjective evaluation of $400 million for gains (i.e., difference of $100 million and $500 million). Thus, the lottery A is preferred in terms of loss aversion.

The inversed-S shaped probability weighting function (Figure 1-1B) suggests that people over-weight small probabilities and under-weight mid-to-high probabilities. This distortion of the objective probabilities also explains the Allais paradox. In lottery B, 1% chance of winning nothing is perceived (over-weighted) more than 1% chance by decision makers. Thus, people want to avoid a risk of non-reward and prefer lottery A.

In summary, expected utility theory, developed by Von Neumann & Morgenstern (1944/1953), prescribes what a rational decision maker should behave. However, a number of economic and psychological studies have revealed that human decision makers do not completely behave rationally, showing a number of cognitive biases (Allais, 1953; Ellsberg, 1961; Kahneman & Tversky, 1979, 1984; Tversky & Kahneman, 1974, 1985). As an alternative model of expected utility theory, prospect theory captures what a human decision maker behave and explains human decision-making process by introducing the value function and the probability weighting function.

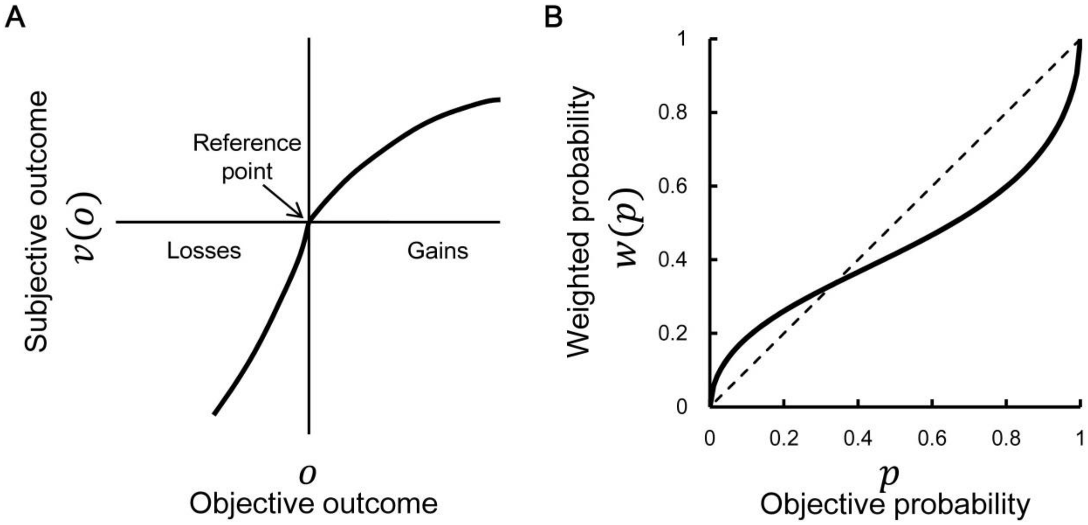

Figure 1-1. Prospect theory. (A) Value function. (B) Probability weighting function.
(Cited and modified from Kahneman & Tversky, 1979 and Tversky & Kahneman, 1992)

1-3. Development of motor decision making studies from economic and psychological studies

As reviewed above, economic and psychological studies have developed the theory of decision making and extensively investigated human behavior in economic decision-making tasks. In recent years, several researchers have focused on decision making involving motor responses and discussed risk-sensitivity in sensorimotor control (for review, see Braun et al., 2011; Trommershäuser et al., 2008; Wolpert & Landy, 2012; Wu et al.,2015). There are two differences between decision-making in economic tasks and that in motor tasks.

First is the continuity of decision making. In economic tasks, individuals are typically faced with a decision between lotteries in which information about rewards and probability are explicitly given (for example, 50% chance of winning \$100 or 100% chance of winning \$50), thus decision-making process is discrete. In contrast, motor tasks require individuals the decision about where they should aim at (for example, a dart player should decide where in a dart board they throw a dart). Therefore, the decision-making process is continuous (Braun et al., 2011).

Second is the internal cause of probability. In contrast to typical economic tasks in which probability of rewards is explicitly given to a decision maker, the probability of rewards is determined by the implicit variability of the motor system. For example, when we decide to throw a dart toward the bull’s eye on a dart board, an outcome of motor responses varies with trial to trial. Therefore, an experience based decision is required (Wu et al., 2009).

Similar to economic and psychological studies, previous studies have focused on whether human decision-making in motor tasks is optimal (risk-neutral) or sub-optimal (risk-sensitive). Here, in Chapter 1-3, I will explain mathematical framework that attempts to prescribe what an ideal decision maker should behave in motor tasks and review the previous findings that claim the optimality of motor decision-making. Based on the motor tasks used in previous studies, I will then point out the research subject that should be addressed in this thesis.

1-3-1. Bayesian decision theory and modeling of optimal motor plan

Bayesian decision theory (BDT; Blackwell & Girshick, 1954) is a mathematical framework for decision-making based on game theory (Von Neumann & Morgenstern, 1944/1953) and is a powerful mathematical method for selecting optimal actions under conditions of uncertainty (Berger, 1980; Maloney & Zhang, 2010). Due to its simple forms, BDT has been applied to model ideal performance in a wide range of visual and motor tasks recently (Maloney & Mamassian, 2009).

Figure 1-2 illustrates one of its applications to a complex movement task that involves visual and motor uncertainty (Trommershäuser et al., 2008). A dinner guest plans to pick up a salt shaker. One possible action plan is schematized as a solid red line. When planning a movement strategy, he should take a positive/negative outcome of motor response (success of grasping/spilling a wine glass) and sensorimotor uncertainty (darkness of candlelight or uncertainty of movement as shown in a red region) into account. Bayesian decision theory prescribes the optimal movement plan as the one for maximizing the expected gain and allows us to model it (Maloney & Mamassian, 2009; Maloney & Zhang, 2010). The decision process of BDT (i.e., components and the functions of BDT) is illustrated in Figure 1-3.

On every turn, the random state of the world w (i.e., an initial position of the arm, positions of a salt shaker and wine glass, darkness of candlelight, and so on) is defined. The state of the world is not completely known to a decision maker. For example, if the candle light is poor, current information about the state of the world is ambiguous. The decision maker has prior distribution of the state of the world $P(w)$ based on past sensory information about table layout. To access the current state of world, the decision maker perceives sensory information v through likelihood function $P(v|w)$ which links the sensory information to the state of the world[1]. For given sensory information, the decision maker selects movement plan S based on his/her decision function $S = d(v)$, which maps from the sensory input to a movement plan. The decision maker then executes the movement plan. Due to inherent motor noise, an actual movement trajectory t is stochastically produced from the executed movement plan though probability distribution $P(t|S)$. Finally, the decision maker experiences a positive or negative gain that is determined by gain function as a function of the actual trajectory and the current state of world $G(t|w)$. In this example, the positive gain is to grasp the salt shaker successfully, and the negative gain is to hit a wine glass. Bayesian decision theory defines the expected gain of the choice of the movement plan S as follow.

$$EG(S) = \iiint G(t|w) \cdot P(t|S) \cdot P(v|w) \cdot P(w)dtdvdw \qquad \text{(1-1)}$$

BDT predicts that the ideal decision maker should choose the plan $S^* = a\underset{S}{\mathrm{rgmax}}\, EG(S)$ in order to maximize the expected gain.

[1] For given prior information about the state of the world and current perceived sensory information, the decision maker obtains the posterior information about the current state of the world and thus can estimate the state of the world (Körding & Wolpert, 2006). Bayes' theorem provides them the posterior distribution $P(w|v)$ by integrating the prior distribution $P(w)$ with the likelihood function $P(v|w)$, defined as $P(w|v) = \frac{P(v|w)\cdot P(w)}{P(v)}$.

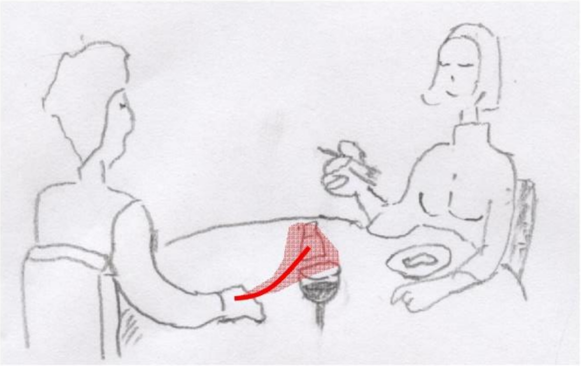

Figure 1-2. Example of applying Bayesian decision theory to sensory motor control.
A dinner guest plans to pick up a salt shaker. The guest might split over a wine glass if an executed movement largely deviates from the planned movement. If executed successfully, the guest will pick up the salt shaker. (Cited and modified from Trommershäuser et al., 2008)

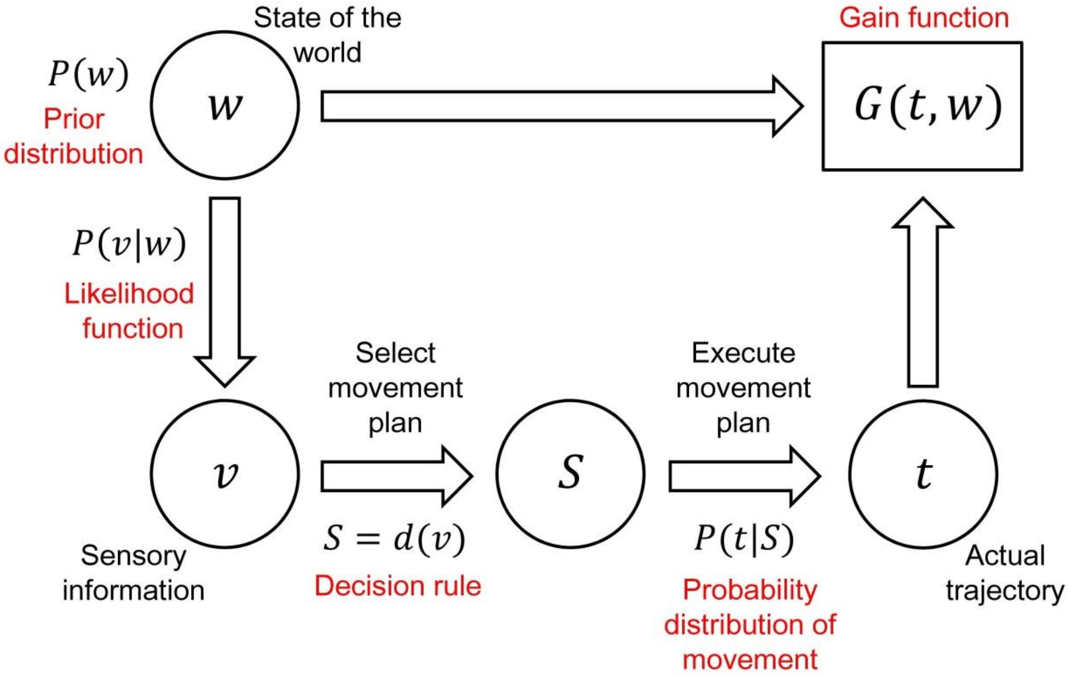

Figure 1-3. Decision process of BDT.

The movement plan that maximizes expected gain depends on both sensory and movement uncertainty. (Cited and modified from Trommershäuser et al., 2008)

1-3-2. Previous studies on decision making in motor tasks

To investigate whether human motor behavior can be explained by Bayesian decision theory, Trommershäuser et al. (2003a; 2003b; 2005) and Trommershäuser, Landy, & Maloney (2006) exposed participants to a pointing task in which explicit rewards was determined by the endpoint of the pointing movement. In this experiment, participants were required to a decision about where in different four regions to aim for (Figure 1-4A), as Wilhelm Tell, a folk hero of Switzerland, was required to shoot an apple on the head of Tell's son with a crossbow. Each region R_i was associated with a monetary reward G_i: the reward only region R_1 with gain G_1, the overlap region R_2 with gain G_2, the penalty only region R_3 with gain G_3, and the background region $R_4$with gain G_4. As participants had to perform the pointing movement within time limits, the endpoints of the movement involved implicitly uncertain and could be approximated by a bivariate Gaussian probability distribution $P(x, y|\bar{x}, \bar{y}, \sigma)$ around an aim point $(\bar{x}, \bar{y})$ with standard deviation σ. Figure 1-4B&C shows simulated endpoints (black dots) for two different aim points (blue & yellow diamond) with same standard deviation. The expected gain per trial is higher when participants aim at the right of the center of the green circle (Figure 1-4C) than when they aim at the center of the green circle (Figure 1-4B). For given participant's motor uncertainty, Trommershäuser et al (2003a, 2003b, 2005, 2006) calculated the expected gain of movement plan (i.e., aim point) $(\bar{x}, \bar{y})$ by integrating the probability of hitting a certain region $P(R_i|\bar{x}, \bar{y}, \sigma) = \int_{R_i} P(x, y|\bar{x}, \bar{y}, \sigma)dxdy$ with the gain of the region G_i, as follow.

$$EG(\bar{x}, \bar{y}) = \sum_{i=1}^{4} G_i \cdot P(R_i|\bar{x}, \bar{y}, \sigma) \qquad (1\text{-}2)$$

As shown in Figure 1-4D, the expected gain was a function of the aim point. The optimal aim point $(\bar{x}^*, \bar{y}^*) = \underset{(\bar{x},\bar{y})}{argmax}\, EG(\bar{x}, \bar{y})$ could be calculated by maximizing the expected gain and this point is shown as a white square in Figure 1-4D (Trommershäuser et al., 2009).

Bayesian decision theory predicts that the ideal movement plan can be achieved if decision maker satisfies following assumptions: 1) he/she has a linear utility function (i.e., a subjective gain is identical with an objective gain), 2) he/she has no distortion of the probability weighting of hitting the regions and estimates own movement variability accurately, and 3) he/she has no computational limitation to maximize the expected gain. In the series of the studies, Trommershäuser et al. (2003a; 2003b; 2005) and Trommershäuser, Landy et al. (2006) varied the location of the circle and amounts of rewards/penalties and found that participant's choice of movement plan (aim point) came close to maximizing the expected gain. In other studies, the model of BDT could also predict participant's motor behavior involving trade-off between movement time and reward (Battaglia & Schrater, 2007; Dean et al., 2007), obstacle avoidance (Hudson et al., 2012), and precise timing (Hudson et al., 2008). These findings indicate that human decision making in motor tasks is rational in contrast to many economic decision making tasks. Although prospect theory (Kahneman & Tversky, 1979; Tversky & Kahneman, 1992) described risk-sensitive decision process by non-linear utility function and distortion of probability weighting function (Figure 1-1A&B), these findings imply risk-neutrality of motor decision since the ideal performance can be built on linear utility function $U(G_i) = G_i$ and linear probability weighing function $w(P(R_i)) = P(R_i)$ (Braun et al., 2011).

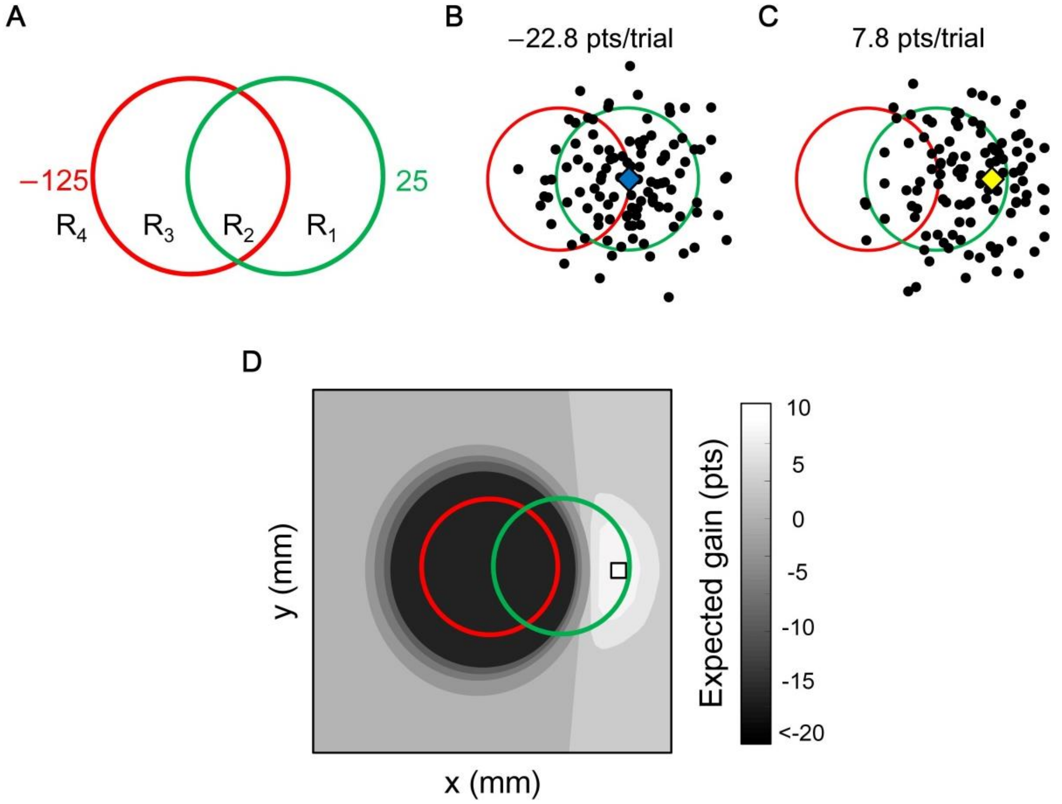

Figure 1-4. Motor decision making task used in previous studies.

(A) Participants are required to decide where they aim to point. Points are determined by the endpoint of pointing movement. (B) Simulated endpoints (black dots) for aiming at the center of the green circle (blue diamond) with motor variability of 5.6 mm. (C) Simulated endpoints for aiming to right of the center of the target circle (yellow diamond) with same motor variability. (D) Expected gain for this motor variability as a function of mean movement endpoint. The maximum expected gain is illustrated as white square.(Cited and modified from Trommershäuser et al., 2009)

1-4. The purpose of the present thesis

Although previous studies suggest the optimality in motor decision making, the configuration of the gain structure is limited and is characterized as symmetric (Wu et al., 2006). In the previous task, participants could obtain either high gain, moderate or negative gain, negative gain, or zero gain (Figure 1-4A). Thus, a constant value of gain is on the edge of a risk of zero gain. However, many sports (for example, tennis, table tennis, baseball, golf, alpine ski, etc.) involve gain structure in which higher performance come with a risk of failure. Since a suboptimal behavior leads to decrease player's performance (Neiman & Lowenstein, 2011), the optimality of motor decision making under such asymmetric gain function should be elucidated. Therefore, the present thesis aimed to investigate characteristics of decision-making in motor tasks with an asymmetric gain function.

1-5. Contents of the present thesis

To this end, I compare actual human behavior with Bayesian ideal behavior and prepare following five studies. First, in Chapter 2, the relationship between the optimality of motor plan and the configuration of the gain function is investigated. Chapter 2 shows that decision-making in a temporal task can be risk-neutral under a symmetric gain function, whereas it can be risk-sensitive under an asymmetric gain function. Chapter 3 demonstrates that this sub-optimality of a motor plan under the asymmetric function does not depend on motor tasks, by showing that humans tend to be risk-sensitive also in a spatial task. In Chapter 4, the effect of learning on a suboptimal motor plan under the asymmetric gain function is shown. This Chapter provides us the strong evidence that it is difficult to learn to aim optimally solely by repeated practice with feedback of motor output in each trial. Bayesian decision theory predicts that suboptimal motor plan would arise if humans have inaccurate knowledge about own motor output distribution. Here, Chapter 5 investigates whether the optimal motor plan can be built on the feedback of motor outputs in whole trial which lead participants to have accurate knowledge about their own motor output distribution. However, Chapter 5 finds that this hypothesis is rejected, which suggests that the suboptimal motor plan arises from the limitation of computational ability for maximizing the expected gain, rather than an inaccurate representation of motor output distribution. Finally, in Chapter 6, the role of dorsolateral prefrontal cortex (DLPFC) on risk-sensitive decision-making is investigated. Chapter 6 demonstrates that risk-seeking strategy is reduced when anodal direct current stimulation over right DLPFC coupled with cathodal stimulation over left DLPFC is applied. This Chapter proposes us possibility that dorsolateral prefrontal cortex is involved in a risky motor decision-making. Taken together, the present thesis concludes that decision-making in motor tasks can be risk-sensitive under the gain structure in which higher gain accompanied with risk of zero gain, possibly due to the human’s computational limitation and the involvement of dorsolateral prefrontal cortex.

Chapter 2.

Relationship between the optimality of temporal motor plan and the configuration of the gain function

This study has been published as:

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2-1. Introduction

The higher performance often goes hand in hand with risk in many sports. Under such situation, it is important to make a decision appropriately. For example, a tennis player requires a spatial action plan about where in a court they should aim; a ski jumper requires a temporal action plan about when they should take off. An executed action is associated with a gain/loss. In ski jumping, the take-off jump should be as close to the edge of the ramp as possible to get the best jump length, while take-off too early or too late decreases jump length (Müller, 2009). However, in whatever action they plan, an executed action is not always equal to the planned one because of motor variability (Kudo et al., 2000; Schmidt et al., 1979; van Beers et al., 2004). Thus, both gain/loss associated with action and uncertainty in motor output should be considered for better decision making.

The mathematical method for selecting an optimal plan under conditions of limited uncertainty is known as statistical decision theory (Berger, 1980; Maloney & Zhang, 2010). In particular, Bayesian decision theory, which is a part of statistical decision theory, is a method for optimizing the expected gain/loss. The expected gain/loss is calculated by integrating the gain/loss function assigned to a certain action over a probability distribution of an executed action given a planned action. The Bayesian decision maker plans the action that optimizes the expected gain/loss for any combination of gain/loss function and motor variability (Hudson et al., 2012).

Previous motor control studies have evaluated the optimality of human motor decision making by comparing Bayesian ideal performance with actual human performance (Hudson et al., 2012; O’Brien & Ahmed, 2013; Trommeshäuser et al., 2003a; Trommeshäuser et al., 2003b; Trommeshäuser et al., 2005; Wu et al., 2006). Some reports have concluded that humans can plan actions that are optimal when considering their own motor variability (Hudson et al., 2012;

Trommeshäuser et al., 2003a; Trommeshäuser et al., 2003b; Trommeshäuser et al., 2005), while other reports have concluded that humans cannot compute the movement strategy that maximizes the expected gain in the presence of such variability (O'Brien & Ahmed, 2013; Wu et al., 2006). Thus, there is inconsistency in published claims concerning the optimality of human action planning.

Two possible factors, –differences in experimental design, and differences in energetic cost–could account for this inconsistency. First, previous studies have reported optimal or suboptimal action plans with different movements and different configurations of the gain function. For example, Trommeshäuser et al. (2003a; 2003b; 2005) and Hudson et al. (2012) have demonstrated optimality in a pointing plan under a gain function in which the magnitude of gain/loss remains constant. In contrast, O'Brien & Ahmed (2013) have shown suboptimal reaching and whole-body movement strategies under an asymmetric gain function in which seeking higher values of gain brings participants closer to scoring zero gain ("falling over the cliff"). Therefore, we cannot directly evaluate the relationship between the optimality of the action plan and the configuration of the gain function because the experimental designs among previous studies differed.

Second, previous studies have mainly treated pointing or reaching movement as executed action (Hudson et al., 2012; O'Brien & Ahmed, 2013; Trommeshäuser et al., 2003a; Trommeshäuser et al., 2003b; Trommeshäuser et al., 2005; Wu et al., 2006). In reaching and pointing movements, energetic cost is proportionally larger as the distance of the required movement is made longer. Because large energetic cost requires large participant effort, energetic cost could be a factor disturbing the measured optimality of action strategies. For example, Hudson et al. (2012) have reported that a discrepancy between ideal and actual performance emerged when optimal but large-cost movements were required during obstacle avoidance (i.e., large excursions).

Here, Chapter 2 used a coincident timing task requiring decision-making and compared the Bayesian ideal performance with actual human performance under four different configurations of gain function including those used O'Brien & Ahmed (2013). In the coincident timing task, energetic cost is constant because the participant just presses a button whatever strategy he/she selects. Thus, I can directly evaluate the relationship between the optimality of action plans and the configuration of the gain function excluding the factor of energetic cost as a possible reason for any discrepancy found. In fact, good agreement between the ideal timing strategy and the actual strategy under a symmetric configuration was found. However, a discrepancy was found under asymmetric configurations. I will discuss possible explanations for this discrepancy. Furthermore, it was also observed that larger trial-by-trial compensation occurred following miss trials than after success trials even though the experienced response errors were of the same magnitude.

2-2. Methods

2-2-1. Participants

Thirty-seven healthy right-handed adults participated in the experiment. Sixteen participants (10 male, 6 female; mean age 28.1 ± 7.8 years) performed Experiment 1-1, twelve (10 male, 2 female; mean age 22.8 ± 2.8 years) participants performed Experiment 1-2, and the remaining nine participants (7 male, 2 female; mean age 21.3 ± 2.2 years) performed Experiment 1-3. All participants were unaware of the purpose of the experiment. This study was approved by the Ethics Committee of the Graduate School of Arts and Sciences, the University of Tokyo.

2-2-2. Experimental task

Figure 2-1 shows the time sequence of a basic experimental task. First, a warning tone was presented to ready the participants for an upcoming trial. Then, a visual cue was presented on a computer screen as a starting signal (14 inches, 1600 × 900 pixels, refresh frequency 60 Hz; Latitude E5420, Dell, Round Rock, TX, USA). The participants were instructed to press a button after presentation of the visual cue. The response time was recorded as the button-press time relative to the onset time of the visual cue. In each trial, the participants gained a point based on "gain function", a function that translated the response time to a certain number of points. The details of the gain function are explained in the following section. The fore period (interval between the warning tone and the visual cue) was randomly varied between 800 ms and 1200 ms in steps of 100 ms. The reference time was 2300 ms after the visual cue and was fixed throughout the experiment. In this experiment, the reference time was associated with gaining 100 points but was not necessarily the time when the participants should respond (see below). The inter-trial interval was 2000 ms. All computerized events were controlled by a program written with LabVIEW software (National Instruments, 2011 Service Pack 1, Austin, TX, USA).

2-2-3. Experimental condition and procedure

In each experimental condition, the participants were required to make a decision about when to press a button to maximize the total gain in 100 trials. The gain for a trial was a function of response time, termed the "gain function." Four conditions were tested, corresponding to different gain functions. The first was characterized as the No Risk condition, which employed a symmetric gain function (Figure 2-2. A). In this condition, a gain for a trial (G) was determined from the following equation.

$$G(t) = \begin{cases} \frac{1}{23}t, \ \ if\ t \leqq 2300 \\ -\frac{1}{23}t + 200, \ \ if\ t > 2300 \end{cases} \qquad (2\text{-}1)$$

In the above equation, *t* represents a response time in milliseconds. When the participants responded earlier than the reference time, they received a number of points that was a positive linear function of response interval. When the participants responded later than the reference time, they received a number of points that was a negative linear function of response interval. A maximum-possible one-trial gain of 100 points could be obtained by responding exactly at the reference time.

The second condition was the Step condition, which also had a symmetric gain function (Figure 2-2.B). In the Step condition, a period of constant gain was on the edge of risk of zero gain both at its start and at its termination as represented by the following equation.

$$G(t) = \begin{cases} 0, \ if & t < 1900 \\ 100, \ if & 1900 \leqq t \leqq 2700 \\ 0, \ if & t > 2700 \end{cases} \qquad (2\text{-}2)$$

The participants received 100 points if they responded within ±400 ms of the reference time. However, zero points were given if they responded at less than reference time -400 ms or at more than reference time +400 ms. I termed these eventualities “miss trials” and when they occurred, the participants were cautioned by an unpleasant alarm and a flashing red lamp on the screen. The volume of the alarm was 71.5 ± 0.4 dB.

The third condition was characterized as the $\text{Risk}_{\text{after}}$ condition, which employed an asymmetric gain function (Figure 2-2.C). In the $\text{Risk}_{\text{after}}$ condition, single-trial gain rose linearly as the reference time approached, then plunged to zero after the reference time and then remained zero thereafter as represented by the following equation.

$$G(t) = \begin{cases} \frac{1}{23}t, \ if\ t \leqq 2300 \\ 0, \ if\ t > 2300 \end{cases} \qquad (2\text{-}3)$$

Earlier than the reference time, the gain function looks the same as that in the No Risk condition. However, zero points were given if the participants responded after the reference time. If they missed, they received the same penalty as in the Step condition. This configuration has been used in O'Brien & Ahmed (2013).

The last condition was the Risk$_{\text{before}}$ condition in which the gain function of the Risk$_{\text{after}}$ condition is mirror-imaged across the reference time (Figure 2-2.D). The gain for a trial was determined from the following equation.

$$G(t) = \begin{cases} 0, \ if\ t < 2300 \\ -\frac{1}{23}t + 200, \ if\ t \geqq 2300 \end{cases} \qquad (2\text{-}4)$$

In contrast to the Risk$_{\text{after}}$ condition, zero points were given if the participants responded before the reference time in the Risk$_{\text{before}}$ condition. Again, if they missed, they received the same penalty as in the Step condition. For trial-by-trial compensation analysis described below, I defined miss trials as trials when the participants received zero points, success trials as any other trials in all four conditions. Of note, all the trials resulted in success in the No Risk condition because the range in success trials was enough large (i.e., it was 4600ms).

In each trial, I provided the participants with feedback information consisting of the relative response time calculated by response time – the reference time, the gain for the trial, and the cumulative total gain. All the participants performed 10 trials for practice. This practice session was conducted to give them a feel for the length of time from the visual cue to the reference time. In this session, I only provided them with the relative response time (i.e., no gain function was applied). After the practice session, all the participants performed 100 trials in the

No Risk condition as a first experimental session. In the second experimental session, the participants who were assigned to Experiment 1-1 performed 100 trials in the $\text{Risk}_{\text{after}}$ condition. The participants who were assigned to Experiment 1-2 performed 100 trials in the $\text{Risk}_{\text{before}}$ condition. Those who were assigned to Experiment 1-3 performed 100 trials in the Step condition. Each condition (No Risk and $\text{Risk}_{\text{before}}$/$\text{Risk}_{\text{before}}$/Step) was conducted as separate experimental session. The participants rested for several tens of seconds between sessions.

Before running each session, I explained the structure of the gain function with a figure visualizing it. Thus, the structure of the gain function was known to the participants before testing. In the figure, following information was also included: 100 points could be gained when the relative response time was 0 ms in the No Risk, $\text{Risk}_{\text{after}}$ and the $\text{Risk}_{\text{before}}$ conditions, and when the relative response time was within ±400 ms of the reference in the Step condition. However, the length of time from the visual cue to the reference time was not described; thus, the participants did not know that it was 2300 ms. Also, before performing the No Risk condition, the participants did not know the gain structure that would be used in the next condition.

I instructed them to maximize total gain in each condition. Thus, they were required to make a decision about when to press a button to maximize the total gain. Actual monetary rewards/penalties were not used (see limitation related to this experimental procedure).

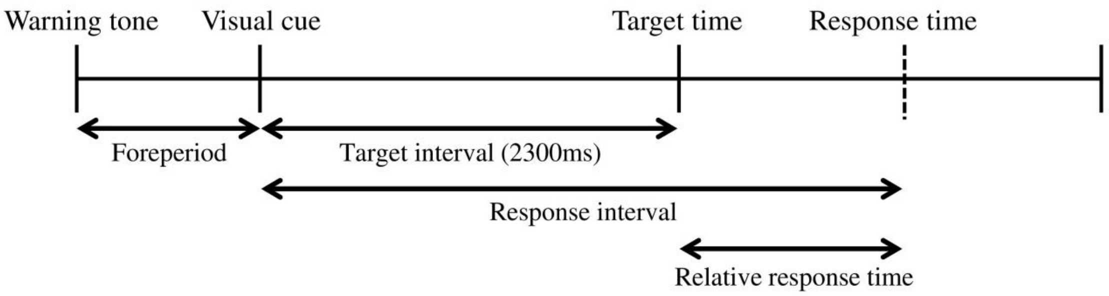


Figure 2-1. The coincident timing task.

First, a warning tone is given. After a fore period of random duration, a visual cue is then presented. The participant is required to press a button after the visual cue. The relative response time (the difference between the response interval and the reference interval) is given to the participant as feedback after every trial.

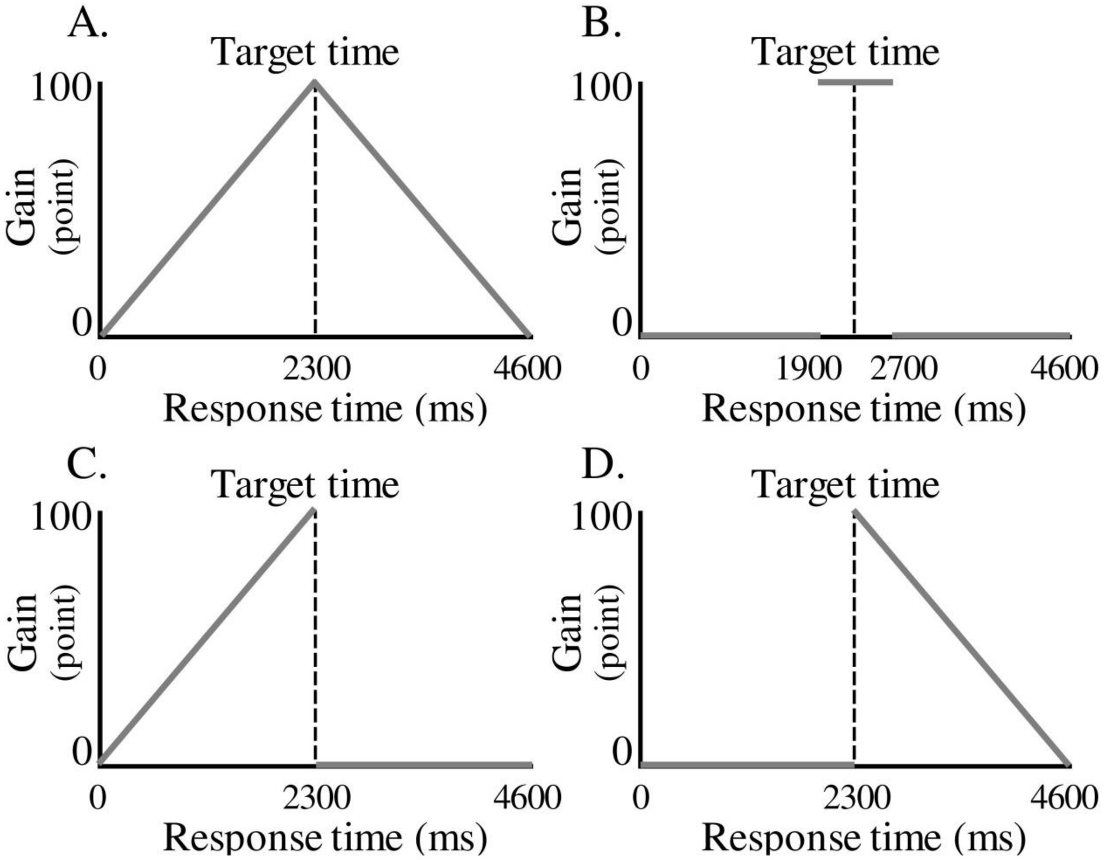


Figure 2-2. Experimental conditions.

(A) A symmetric gain function in the No Risk condition. A gain for a trial is determined by the magnitude of the response time. (B) A symmetric gain function in the Step condition. (C) An asymmetric gain function in the $\mathrm{Risk}_{\mathrm{after}}$ condition. (D) An asymmetric gain function in the $\mathrm{Risk}_{\mathrm{before}}$ condition.

2-2-4. Model assumptions

I calculated the ideal strategy that maximizes the expected gain by a Bayesian decision-theoretic approach for each participant and for all conditions (Hudson et al., 2012). The model consisted of two sets and two functions. The two sets were: possible response strategy T (motor decision), and executed response time t (motor output). The two functions were: probability distribution of executed response $P(t|T)$, and gain function $G(t)$. Given a particular planned strategy, a particular response is stochastically executed. This is considered the uncertainty in motor output. In this study, I assumed that the produced response time t is distributed around the planned response time T according a Gaussian distribution (see Supplementary Table 2-1) as follows.

$$P(t|T) = \frac{1}{\sqrt{2\pi\sigma^2}} exp\left[-\frac{(t-T)^2}{2\sigma^2}\right] \qquad \text{(2-5)}$$

Then, given execution of a particular response time, the gain is given according to the gain function $G(t)$. Given both $P(t|T)$ and $G(t)$, the expected gain $EG(T)$ as a function of planned response time T is calculated by the following equation.

$$EG(T) = \int_{-\infty}^{\infty} G(t) \cdot P(t|T) dt \qquad \text{(2-6)}$$

Once I had measured the response variance σ for each participant and condition, I could calculate the optimal mean response time T_{opt} by maximizing equation (2-6). A Bayesian decision maker chooses a response time T_{opt} for any given gain function $G(t)$ and response variance σ. This can be regarded as a theoretical risk-neutral optimal response.

2-2-5. Estimation of 95% confidence interval of optimal response time

Furthermore, I estimated the 95% confidence interval of the optimal mean response time T_{opt} by bootstrapping (3000 resamples) for the $\text{Risk}_{\text{after}}$ and the $\text{Risk}_{\text{before}}$ conditions. I then examined whether the actual response time is within this 95% confidence interval in the Risk$_{\text{after}}$ condition and in the Risk$_{\text{before}}$ condition. In a range from $\sigma = 0$ to $\sigma = 400$ in steps of $\sigma = 1$, I first calculated each optimal mean response time $X_{opt1}(\sigma_0)$, $X_{opt2}(\sigma_{0.001})$, $\cdots$, $X_{opt400}(\sigma_{0.4})$ by maximizing equation (2-6). Here focusing on $X_{opt1}(\sigma_0)$, I simulated 100 trials of a task execution responding by this optimal mean response time and having this response variance (in this case X_{opt1}= 2300, $\sigma = 0$) using a MATLAB *randn* function. I repeated this process 3000 times and obtained bootstrap samples $x_1 = (x_{1t1}, x_{1t2}, \cdots, x_{1t100})$, $x_2 = (x_{2t1}, x_{2t2}, \cdots, x_{2t100})$, $\cdots$, $x_{3000} = (x_{3000t1}, x_{3000t2}, \cdots, x_{3000t100})$. For each bootstrap sample x_b $(b = 1, 2, \cdots, 3000)$, I calculated the average value of its samples $\hat{\mu}_b = \frac{1}{100} \cdot \sum_{i=1}^{100} (x_{bti})$. After sorting these average samples $\hat{\mu}_b (b = 1, 2, \cdots, 3000)$ in ascending order, I defined a 2.5 % and a 97.5 % point in these samples as the 95 % confidence interval in optimal mean response time T_{opt}. By repeating the above processes from $X_{opt1}(\sigma_0)$ to $X_{opt400}(\sigma_{400})$, I estimated the 95 % confidence intervals of each optimal mean response time.

If the observed mean response times were within these 95 % confidence intervals, I would conclude that the participant plans optimal and risk-neutral timing strategies. In the Risk$_{\text{after}}$ condition, observed times longer than the confidence intervals would indicate suboptimal and risk-seeking strategies. Observed times shorter than the confidence intervals would indicate suboptimal and risk-averse strategies.

2-2-6. Optimal response times calculated from the measured distributions

Although I had confirmed that the response distributions were Gaussian (see Supplementary Table 2-1), I also calculated optimal mean response time for the Risk$_{\text{after}}$ and the Risk$_{\text{before}}$ conditions using the measured response distributions. In the Risk$_{\text{after}}$ condition (Figure

2-3.A, upper panel), once I had obtained the response distribution I simply shifted it back and forth to identify the maximal total gain for that distribution (Figure 2-3.A, lower panel). In Figure 2-3.A, I show the case of shifting the measured distribution back. I defined the optimal mean response time as the mean response time of the optimized distribution (gray solid line in Figure 2-3.A). The estimated optimal mean response time was always earlier than the reference time in the $\text{Risk}_{\text{after}}$ condition. The difference between the estimated optimal response time and the reference time reflected each participant's own variance in response time, (i.e., the larger one's variance, the earlier the optimal response time, and vice-versa. This effect is visualized in Figure 2-5 as the solid curve).

In Figure 2-3.B, the black arrow indicates the total gain when the measured distribution is not shifted and the gray arrow indicates the highest total gain possible for that distribution under shifting. The two-headed arrows in Figure 2-3.A and Figure 2-3.B represent the optimal shift size.

Finally, I compared the estimated optimal mean response times with the observed mean response times (black solid line in Figure 2-3.A). In this case, the observed time was closer to the reference time than optimal, indicating risk-seeking. I also applied this approach to the $\text{Risk}_{\text{before}}$ condition. I compared the mean, as opposed to median optimal and observed times because the measured distributions were Gaussian.

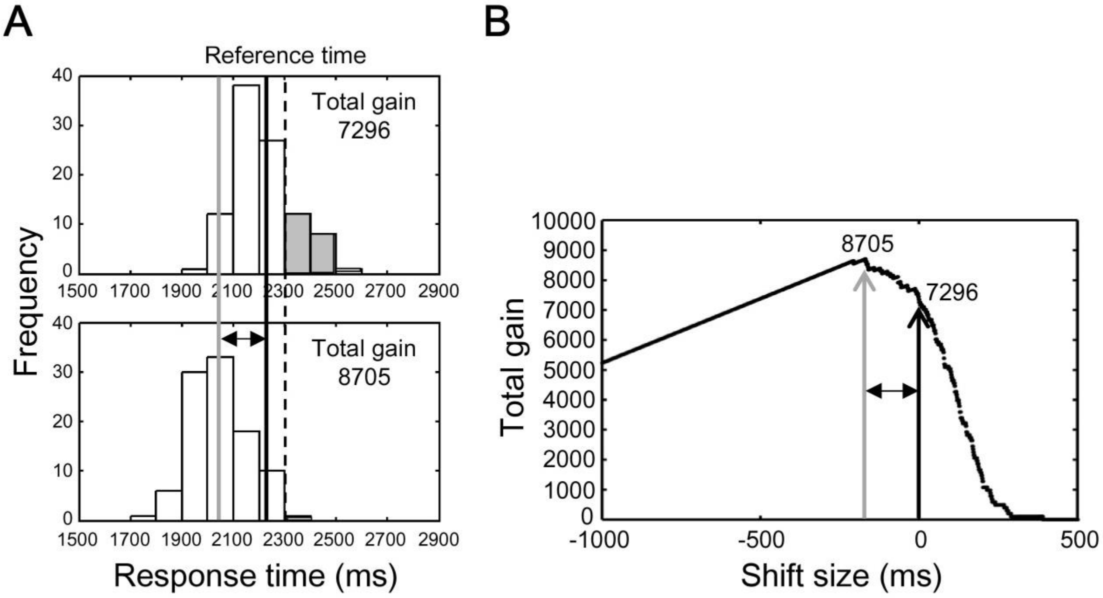


Figure 2-3. Procedure for estimating optimal response time.

(A) Upper panel shows the response distribution obtained in the $\mathrm{Risk}_{\mathrm{after}}$ condition. The black solid line indicates the observed mean response time and the dotted line is the reference time. Lower panel shows the distribution after shifting along the time axis to maximize total gain. The gray solid line indicates the optimal mean response time estimated in this way. In this case, the observed mean response time is found to locate closer to the reference time than optimal time (risk-seeking behavior), thus the total gain was reduced by some miss trials (gray bars). (B) Black arrow indicates the total gain (7296 points) when the distribution in the $\mathrm{Risk}_{\mathrm{after}}$ condition is not shifted. The distribution was shifted until the highest total gain (8705 points; gray arrow) was obtained. This optimal shift size is represented by the two-headed arrow. The estimated optimal mean response time (gray solid line in A) is the sum of the observed mean response time and the optimal shift size.

2-2-7. Trial-by-trial compensation strategy

In addition to determining the response time strategies based on all trials, I examined compensation against the most recent response error based on a trial-by-trial analysis. These results were then compared between/within the No Risk and the $\text{Risk}_{\text{after}}$/$\text{Risk}_{\text{before}}$ conditions. The magnitude of the response error experienced on the current trial is known to influence the response in the following trial (Scheidt et al., 2001; Thoroughman & Shadmehr, 2000). Thus, the compensation size in the following trial can be proportional to the current magnitude of response error. Additionally, it has been shown that humans adjust future motor behavior according to rewarding and non-rewarding outcomes experienced (Wrase et al., 2007). Therefore, in addition to the compensation strategy against response error, I hypothesized that the compensation size following miss trials would be larger in the $\text{Risk}_{\text{after}}$/$\text{Risk}_{\text{before}}$ conditions than the compensation size following success trials in the No Risk condition.

I defined the compensation on the current trial, trial n, by subtracting the response time on the current trial, from that on the following trial, trial $n+1$, as in equation (2-7).

$$Compensation_n = RT_{n+1} - RT_n \qquad \text{(2-7)}$$

I supposed that the compensation occurs around mean response time in both conditions, thus I defined response error as response time – mean response time in this analysis. The compensation size was anticipated to depend on the magnitude of response error (in other words, the magnitude of deviation between the current response time and mean response time).

To compare the compensation size on the following to miss/success trials, I defined the absolute value of the difference between mean response time in the $\text{Risk}_{\text{after}}$/$\text{Risk}_{\text{before}}$ condition and the reference time as "M" for convenience, and sorted trials into following four bins, $-2\text{M} < error_n \leq -\text{M}$ (bin 1), $-\text{M} < error_n \leq 0$ (bin 2), $0 < error_n \leq \text{M}$ (bin 3), and $\text{M} <$

$error_n \leq 2\mathrm{M}$ (bin 4) for Experiment 1-1 and $-2\mathrm{M} \leq error_n < -\mathrm{M}$ (bin 1), $-\mathrm{M} \leq error_n < 0$ (bin 2), $0 \leq error_n < \mathrm{M}$ (bin 3), and $\mathrm{M} \leq error_n < 2\mathrm{M}$ (bin 4) for Experiment 1-2. Figure 2-4 shows the error distributions separated by the bins. With these procedures, I can evaluate the compensation sizes based on same magnitude of response error between conditions. Scaling by "M" also allows data from different participants to be combined. The last bin in Experiment 1-1 and the first bin in Experiment 1-2 are in the areas that result in miss trials in the $\mathrm{Risk_{after}}$/$\mathrm{Risk_{before}}$ conditions. Errors $-2\mathrm{M}$ or less and more than 2M in Experiment 1-1 and errors less than $-2\mathrm{M}$ and $2\mathrm{M}$ or more in Experiment 1-2 were excluded from the analysis because only small numbers of trials were obtained within these ranges. I collected errors on trial *n* in each bin and calculated the average compensation size in each bin. Repeating this procedure for each participant and condition, I compared the average compensation size across the participants against the magnitude of response error between/within conditions for each bin. Because the distributions of the compensation sizes across the participants were Gaussian, I calculated the average value.

2-2-8. Data analysis

I conducted paired t-tests to examine the significance of differences between optimal and observed values for response time and total gain in all conditions. I also conducted two-way repeated-measures ANOVA to determine differences in trial-by-trial compensation strategy between the No Risk condition and the $\mathrm{Risk_{after}}$/$\mathrm{Risk_{before}}$ conditions. A p value of < .05 was regarded as statistically significant. Cohen's *d* measure for the *t*-test was calculated to determine the magnitude of mean differences. Trials with response times more than ±2.5 standard deviations from the mean were excluded from the analysis as outliers. Average number of trials excluded across the participants and two conditions was 2.4±1.5 in Experiment 1-1, 2.3±1.3 in Experiment 1-2, and 1.7±0.7 in Experiment 1-3.

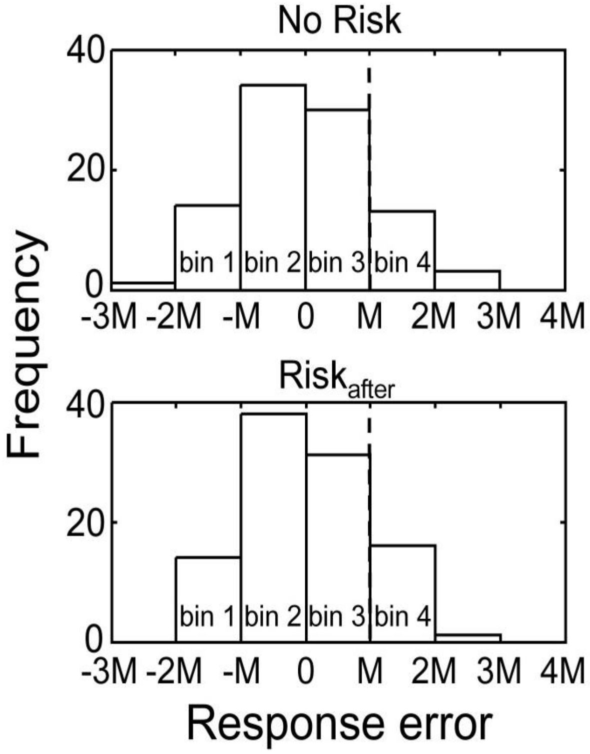


Figure 2-4. Procedure of trial by trial analysis.

Upper panel shows the response error distribution obtained in the No Risk condition. Lower panel shows the response error distribution obtained in the $\text{Risk}_{\text{after}}$ condition. The value of “0” in the x-axis corresponds to mean response error in both conditions. For comparable analysis between conditions, I sorted trials into four bins separated by the range “M”. *“M”* indicates the absolute value of the difference between mean response time in the $\text{Risk}_{\text{after}}$/$\text{Risk}_{\text{before}}$ condition and the reference time. It allows data from different participants to be combined. The average value of *“M”* across the participants was 153.8 ± 42.4 in Experiment 1 and 194.5 ± 40.5 in Experiment 2. In this example, bin 4 (i.e., the range: $\mathbf{M} < \boldsymbol{error_n} \leq \mathbf{2M}$) was the area of miss trial in the $\text{Risk}_{\text{after}}$ condition. In contrast, the same bin was the area of the success trial in the No Risk condition. We especially focused on the compensation size following to errors included in these ranges.

2-3. Results

2-3-1. Discrepancies with optimal strategy

First of all, I found discrepancies between the Bayesian ideal strategy and the actual human strategy in the $\text{Risk}_{\text{after}}$ and the $\text{Risk}_{\text{before}}$ conditions. The observed mean response times and the optimal mean response times calculated from the measured distributions were plotted against the standard deviation (SD) of response time in the $\text{Risk}_{\text{after}}$ condition for all sixteen participants (Figure 2-5A). The optimal mean response times calculated by the Bayesian model and their 95 % confidence intervals were also plotted. As shown in Figure 2-5A, the optimal mean response time moves further from the reference time as response variance increases. However, for all participants, except one, the observed mean response time was closer to the reference time than the optimal mean response time calculated either from the Bayesian-theoretical 95 % confidence interval or from the measured distribution. This result suggests that the participants took higher-than-optimal risks given their own variance in response time, which is classified as a sub-optimally risk-seeking tendency.

The participants were also suboptimal in the $\text{Risk}_{\text{before}}$ condition in the sense that they were in general faster to respond than predicted by the optimal model (Figure 2-5B). In the $\text{Risk}_{\text{before}}$ condition, the optimal time is later than the reference time. I found that all 12 participants responded closer to the reference time than the Bayesian-theoretical 95 % confidence interval for the optimal mean response time and the optimal response time calculated from the measured distribution. Therefore, a risk-seeking strategy was shown under an asymmetric gain function regardless of the location of the penalty region.

I also found that the SD of the response time was significantly correlated with that of the observed mean response time in the $\text{Risk}_{\text{before}}$ condition (r = 0.59, $p < .05$; but was not significantly correlated in the $\text{Risk}_{\text{after}}$ condition, r = - 0.36, p = .17). Thus, in the $\text{Risk}_{\text{before}}$ condition, participants who had large response variance responded further to the reference time than those who had small variance. This result raises a possibility that the participants might have chosen response times reflecting the size of their own response variance. However, their timing strategy was not optimal from the perspective of Bayesian decision theory.

2-3-2.The effect of the symmetry of the gain function

I then compared the optimal mean response time estimated by the Bayesian model with the observed mean response time in all four conditions (Table 2-1). Paired *t*-tests showed that across participants, the optimal mean response time was not significantly different from that observed in the No Risk (t [36] = - 0.08, p = .94, d = - 0.02) and the Step conditions (t [8] = 1.76, p = .12, d = 0.87). However, the observed mean response time in the $\text{Risk}_{\text{after}}$ condition was significantly longer than the optimal mean response time (t [15] = - 8.00, p < .001, d = - 2.35), and was significantly shorter in the $\text{Risk}_{\text{before}}$ condition (t [11] = 6.68, p < .001, d = 1.95). Thus, the participants planned optimal timing strategies only under a symmetric gain functions.

Looking at total gain, the average value of the observed total gain across participants was not significantly different from that of the optimal total gain in the Step condition (t [8] = - 0.33, p = .75., d = - 0.08). The average observed total gain was significantly smaller than the average optimal gain in the No Risk (t [36] = 2.38, p < .05, d = 0.14), the $\text{Risk}_{\text{after}}$ (t [15] = 7.14, p < .001, d = 1.61), and the $\text{Risk}_{\text{before}}$ (t [11] = 6.68, p < .001, d = 0.67) conditions. Although the total gain was significantly smaller than the optimal gain in the symmetric No Risk condition, its effect size was apparently small compared with the asymmetric $\text{Risk}_{\text{after}}$ and $\text{Risk}_{\text{before}}$ conditions.

Taken together, I confirm that an optimal strategy for maximizing expected gain could be computed under a symmetric gain function, but not under an asymmetric gain function.

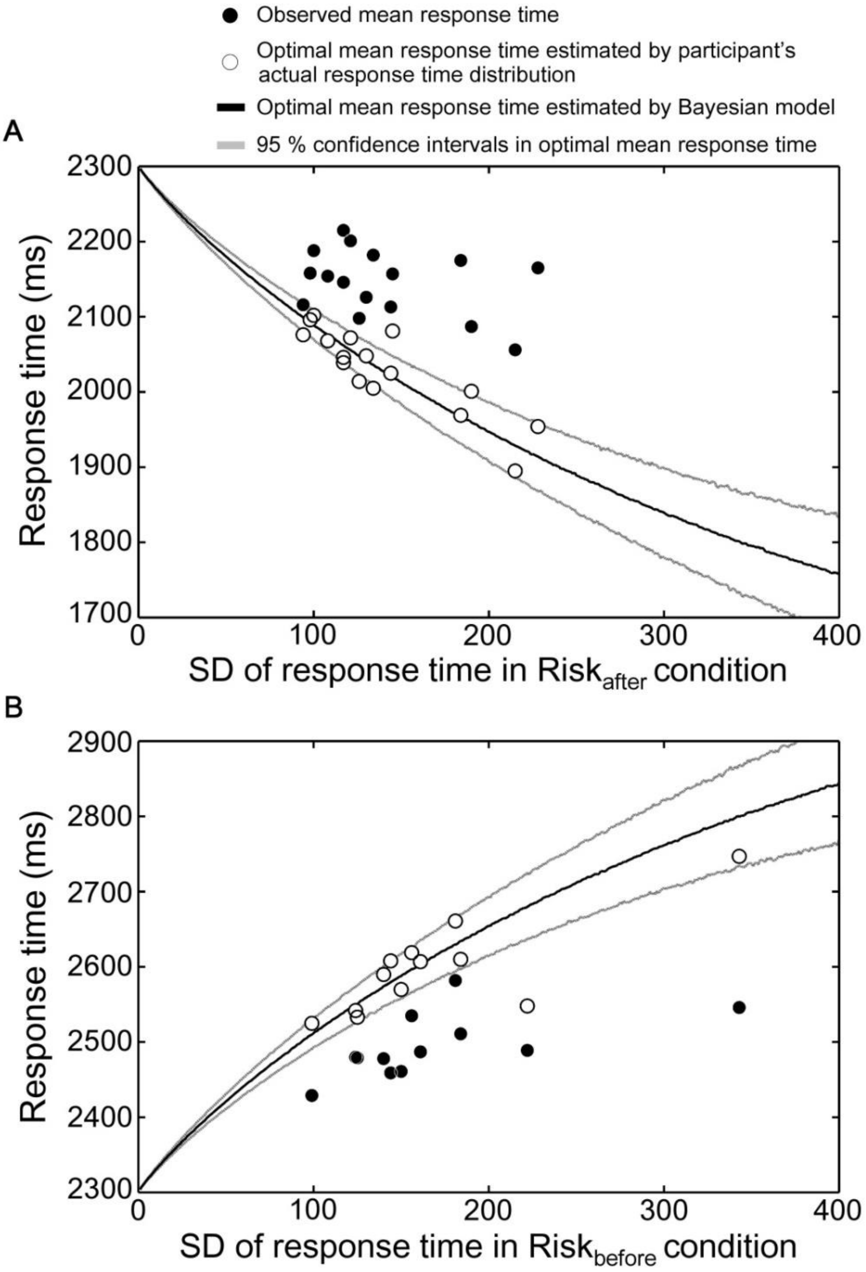


Figure 2-5. The participants adopt a risk-seeking strategy.

(A) Results in the Risk$_{after}$ condition, one dot of each color corresponds to a participant. Theoretically, the optimal mean response time must be shorter than the reference time as an increasing function of the variability of one's response time. However, the observed mean response times (filled circles) are closer to the reference time than optimal. Open circles indicate optimal mean response times estimated by shifting the participant's actual response time distributions. Black curve indicates the optimal mean response time estimated by a Bayesian model (Equation 2-6). (B) Results in the Risk$_{before}$ condition. The observed response times are again closer than optimal to the reference time.

Table 2-1. Suboptimal strategies are adopted under asymmetric gain functions.

Optimal response time and optimal total gain were calculated with a Bayesian model (equation 6). All data shown are averages across the participants ± standard deviation of the mean. * indicates *p* < .05 and *** indicates *p* < .001.

Gain function	Condition	N	Optimal response time (ms)	Observed response time (ms)	Effect size (d)	Optimal total gain (point)	Observed total gain (point)	Effect size (d)
Symmetry	No Risk	37	2300.0 ± 0.0	2300.9 ± 72.9	- 0.02	9104.0 ± 216.0	9070.6 ± 245.8 *	0.14
	Step	9	2300.0 ± 0.0	2285.3 ± 23.9	0.87	9585.6 ± 158.4	9600.0 ± 194.4	- 0.08
Asymmetry	$\text{Risk}_{\text{after}}$	16	2029.5 ± 56.1	2146.2 ± 42.4 ***	- 2.35	8382.7 ± 347.8	7686.8 ± 501.3 ***	1.61
	$\text{Risk}_{\text{before}}$	12	2611.8 ± 69.9	2495.2 ± 40.3 ***	2.04	8160.6 ± 442.3	7833.8 ± 556.9 ***	0.65

2-3-3. Altering the timing strategy thorough trials

I analyzed timing strategy on a whole block of 100 trials and showed its sub optimality in the $\text{Risk}_{\text{after}}$ and the $\text{Risk}_{\text{before}}$ conditions. However, there is a possibility that the participants gradually alternated the strategy thorough trials. To investigate this possibility, I compared the mean response time over the first 50 trials with the mean over the last 50 trials across participants. Paired *t*-tests showed that early and late mean response times were not significantly different in the $\text{Risk}_{\text{after}}$ condition (t [15] = 1.48, p = .16) and the $\text{Risk}_{\text{before}}$ condition (t [11] = 0.53, p = .61). Furthermore, I conducted paired *t*-tests in each participant excluding trials that were classified as outliers. The results showed that early and late mean response times were significantly different for only 1 out of 16 participants in the $\text{Risk}_{\text{after}}$ condition (t [47] = 2.10, p < .05 for P13), and for 2 out of 12 participants in the $\text{Risk}_{\text{before}}$ condition (t [47] = - 2.76, p < .01 for P 18; t [47] = 2.68, p < .01 for P22). Therefore, I concluded that participants did not change timing strategy through trials. This result is consistent with previous studies claiming no evidence of learning effects on movement plans (O'Brien & Ahmed, 2013; Trommershäuser et al., 2003b; Trommershäuser et al., 2005; Wu et al., 2006).

2-3-4. Trial-by-trial compensation strategy

Finally, I compared trial-by-trial compensation strategies between the No Risk and the $\text{Risk}_{\text{after}}$/$\text{Risk}_{\text{before}}$ conditions. To this end, in Figure 2-6A I plotted the average compensation size across participants against the magnitude of response error on the previous trial in Experiment 1-1. I performed two-way repeated-measures ANOVA on the compensation size. The levels were condition (2: $\text{Risk}_{\text{after}}$ condition and No Risk condition) and bin (4: bin 1-4). I found a main effect of bin (F [1.63, 24.46] = 185.02, p < .001). Thus, the average compensation size changed based on the experienced response error. Furthermore, I also found an interaction effect (F [2.23, 33.52] = 6.36, p < .01) and a simple main effect of condition in bin 4 (F [1, 15] = 10.78, p < .01), but not in any other bins (Fs [1, 15] < 4.16, ps > .05). Of note, miss trials in the $\text{Risk}_{\text{after}}$ condition are included in bin 4 (i.e., the range: $\text{M} < error_n \leq 2\text{M}$). Moreover, in bin 4, the average compensation size in the $\text{Risk}_{\text{after}}$ condition was significantly larger than that in the No Risk condition (t [15] = - 3.28, p < .01, d = - 1.03). These results suggest that the participants used statistically the same compensation strategy following success trials (bins 1 to 3 in both conditions), but compensated more strongly following miss trials (bin 4 in the $\text{Risk}_{\text{after}}$ condition) compared with success trials (bin 4 in the No Risk condition), even though response errors in both bins were of the same magnitude (see Supplementary Figure 2-1).

Larger compensation after misses was also seen in Experiment 1-2 (Figure 2-6C). Again, I performed two-way repeated-measures ANOVA on the compensation size. I found a main effect of bin (F [1.59, 17.48] = 192.30, p < .001) and an interaction effect (F [3, 33] = 4.12, p < .05). I also found a simple main effect of condition in bin 1 (F [1, 11] = 6.90, p < .05), but not in any other bins (Fs [1, 11] < 2.70, ps > .05). Bin 1 (i.e., the range: $-2\text{M} \leq error_n < \text{M}$) is in the area of miss trials in the $\text{Risk}_{\text{before}}$ condition. Similarly to Experiment 1-1, the average compensation size in the $\text{Risk}_{\text{before}}$ condition was larger than that in the No Risk condition in bin 1 (t [11] = 2.63, p < .05, d = 0.80). Therefore, I confirmed larger compensation following miss trials as a robust result regardless of the location of the penalty region.

I also confirmed that larger compensation occurred within the same Risk conditions. Paired t- test revealed that the absolute value of the average compensation size in bin 1 was significantly larger than that in bin 4 within the $\text{Risk}_{\text{before}}$ condition (t [11] = 3.45, p < .01, d = 0.91; individual data were shown in Figure 2-6D). Within the $\text{Risk}_{\text{after}}$ condition, the absolute compensation size in bin 4 was marginally significantly larger than that in bin 1 (t [15] = - 1.78, *p* = .096, *d* = - 0.53; individual data were shown in Figure 2-6B). Magnitude of response errors was same in bin 1 and bin4 but sign of errors was different. There was not significant difference between bin 1 and bin 4 in the No Risk condition in Experiment 1-1 (*t* [15] = 0.75, *p* = .47, *d* = 0.18) and in Experiment 1-2 (*t* [11] = - 0.41, *p* = .69, *d* = - 0.15).

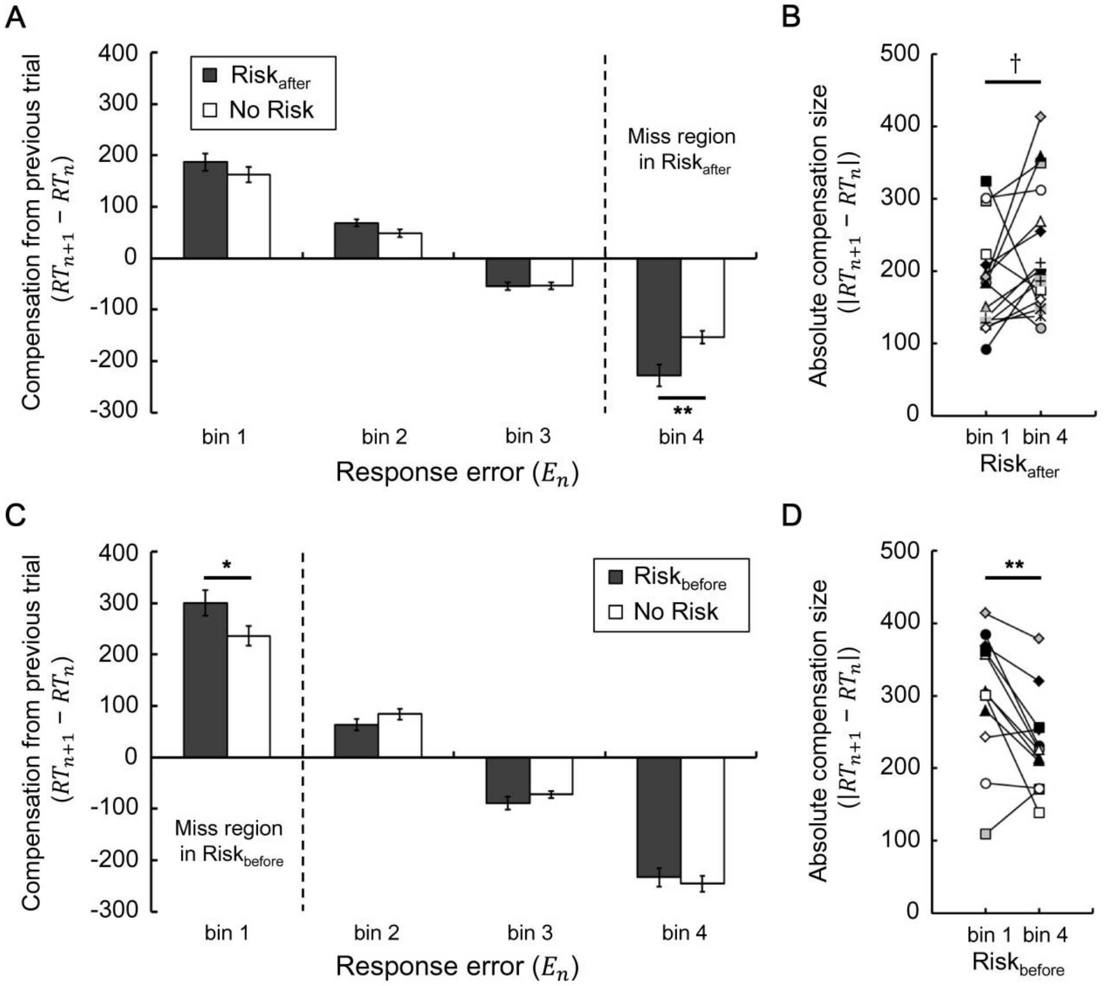


Figure 2-6. Trial-by-trial compensation strategy adopted by the participants.

(A) Result of Experiment 1. Compensation based on feedback from the previous trial depends on the magnitude of the experienced response error. The average compensation across participants is plotted against the magnitude of response error for the Risk$_{after}$ and No Risk conditions. The average compensation in the Risk$_{after}$ condition is to significantly shorter times than that in the No Risk condition in bin 4 (penalty region in the Risk$_{after}$ condition), which indicates that participants overcompensate following miss trials. (B) Individual data in the Risk$_{after}$ condition, each colored symbol corresponds to a participant. (C) Result of Experiment 2. The same tendency is observed in the Risk$_{before}$ condition. The average compensation in the Risk$_{before}$ condition is to significantly longer times than that in the No Risk condition in bin 1 (penalty region in the Risk$_{before}$ condition). (D) Individual data in the Risk$_{before}$ condition.

† indicates $p < .10$, * indicates $p < .05$, and ** indicates $p < .01$. Error bars indicate standard error of the mean.

2-4. Discussion

Chapter 2 directly evaluated the relationship between the optimality of action plans and the configuration of the gain function. With the coincident timing task, I could exclude the energetic cost factor, which might disturb an optimal action plan. Compared with Bayesian optimal timing strategy, the participants planned suboptimal strategies under asymmetric configurations. They tended to respond closer than optimal to times presenting the risk of zero gain. Under symmetric configurations, good agreement between the observed and optimal strategies was found. Furthermore, larger compensation occurred following miss trials compared with success trials even though the experienced response errors were of the same magnitude.

I investigated whether humans can calculate an optimal timing strategy that maximizes the expected gain under four configurations of the gain function. In the Step condition, a constant value of gain was on the edge of risk of zero gain. The gain function has a symmetric configuration in this condition. Most of the relevant previous studies have used this type of gain function and have reported optimal movement planning (Hudson et al., 2012; Trommeshäuser et al., 2003a; Trommeshäuser et al., 2003b; Trommeshäuser et al., 2005). I likewise showed that strategies were optimal in the Step condition. In the $\mathrm{Risk}_{\mathrm{after}}$ condition, higher values of gain come with higher risk. I found a discrepancy between the ideal Bayesian model and actual strategy in the $\mathrm{Risk}_{\mathrm{after}}$ condition, participants showing a risk-seeking strategy. My finding is consistent with a previous study that reports risk-seeking strategy under a similar gain function during reaching and whole-body movement tasks (O’Brien & Ahmed, 2013). In addition to the $\mathrm{Risk}_{\mathrm{after}}$ condition, I applied the $\mathrm{Risk}_{\mathrm{before}}$ condition in which the configuration of the $\mathrm{Risk}_{\mathrm{after}}$ condition was inverted with respect to time. I confirmed a risk-seeking strategy even in the $\mathrm{Risk}_{\mathrm{before}}$ condition. Therefore, these results suggest that human action plans tend to be suboptimal under situations in which higher values of gain occur closer to zero gain regardless of the location of risk. On the other hand, action plans could be optimal under situations in which a constant value of gain was close to zero gain.

A symmetric gain configuration was applied in the No Risk and Step conditions, while an asymmetric configuration was applied in the $\text{Risk}_{\text{after}}$ and $\text{Risk}_{\text{before}}$ conditions. Wu et al. (2006) have investigated the endpoint of pointing movements under both symmetric and asymmetric expected gain landscape. Theoretically, the optimal endpoint in that study lay within the target circle under a symmetric expected gain landscape, similar to the task used in Trommershäuser et al (2003a; 2003b; 2005), but lay within the penalty circle and did not cover the target circle under an asymmetric expected gain landscape. These researchers showed that an intuitive strategy to aim within the target circle could be adopted, but a counterintuitive strategy to aim within the penalty circle could not be adopted. Even in this experiment, the participants might not easily detect when they should press a button because optimal response time depends on response variance under an asymmetric configuration of the gain function. Therefore, the findings indicate a limitation on information processing and computational ability in decision making under uncertainty in motor output as well as in economic decision making (Simon, 1956).

In the field of behavioral economics, prospect theory (Kahneman & Tversky, 1979) and cumulative prospect theory (Tversky & Kahneman, 1992) claim that irrational decision making is caused by a distortion of probability weighting from the actual probability and a distortion of subjective utility from the actual gain/loss (Figure 1-1). Prospect theory gives two reasons for risk-seeking behavior.

One reason would be an inappropriate estimation of the participant’s own variance in response time (Nagengast et al., 2011b; O’Brien & Ahmed, 2013; Wu et al., 2009). Wu et al., (2009) have shown that participants under-weighted small probabilities and over-weighted large probabilities when they made a decision whether to point to a riskier target bar or a safer target bar. O’Brien & Ahmed (2013) have also shown a similar distortion of probability weighting during a reaching task. These reports indicate that the participants might have believed that they had smaller response variability than they actually did. Such an inappropriate estimation of their own variance would have influenced them to approach the penalty zone more closely.

Before performing the $\text{Risk}_{\text{after}}/\text{Risk}_{\text{before}}$ condition, participants had only experienced 100 trials in the No Risk condition. Thus, they may not have had enough experience with the task to know their own response variance, but the report of Zhang et al. (2013) calls into question the idea that more practice would have helped. These researchers have shown that the distribution of a reaching endpoint was recognized as an isotropic distribution rather than the actual anisotropic distribution, and that this inaccurate estimation persisted even after extensive practice. This report indicates that an inappropriate estimation of one’s own variance is not necessarily caused by lack of practice. Thus, the ability to recognize one’s own variance in motor output appropriately may have limitations.

The second reason would be inappropriate evaluation of gain/loss (Lee, 2005; O’Brien & Ahmed, 2013). Risk-seeking in decision making arises when the subjective utility of gain is overvalued against the objective value (Lee, 2005). Here, higher values of gain came with a higher risk of zero gain in the $\text{Risk}_{\text{after}}/\text{Risk}_{\text{before}}$ conditions. O’Brien & Ahmed (2013) showed that most participants overvalued point reward and undervalued point penalty under this type of gain function. This inappropriate evaluation of gain/loss would also influence the participants to respond closer to the point where gains of zero began. However, I could not distinguish which distortion most affected risk-seeking behavior using the above analyses. Thus, the remaining issue is to specify them using other experimental paradigms.

I also investigated differences in trial-by-trial compensation strategy between/within the No Risk and the $\text{Risk}_{\text{after}}$/$\text{Risk}_{\text{before}}$ conditions. I found larger compensations following miss trials compared with success trials between the No Risk and the $\text{Risk}_{\text{after}}$/$\text{Risk}_{\text{before}}$ conditions with the same magnitude of response errors (see Supplementary Figure 2-1). The sign of response errors was same in comparison between the conditions. In comparison within the $\text{Risk}_{\text{after}}$/$\text{Risk}_{\text{before}}$ conditions, I also found that larger compensations occurred following miss trials compared with success trials with different sign of response errors. I assume that this is because of motivation to avoid consecutive misses.

Error feedback is necessary for motor adaptation (motor learning). Previous studies have investigated how the magnitude of error influences subsequent adaptation. These studies have reported that the size of the adaptation has a linear relationship with the magnitude of past errors (Scheidt et al., 2001; Thoroughman & Shadmehr, 2000). Linear adaptation against error is an element in minimizing future errors. However, recent studies have shown that motor adaptation does not depend simply on the magnitude of error. A non-linear relationship has been observed when the subjective value, directional bias, statistical properties, and relevance of errors are experimentally manipulated (Fine & Thoroughman, 2007; Trent & Ahmed, 2013; Wei & Körding, 2009).

In this task, the subjective value of error (Trent & Ahmed, 2013) was different between conditions. Errors over/within the reference time were cautioned in the $\text{Risk}_{\text{after}}$/$\text{Risk}_{\text{before}}$ condition, while same magnitude of errors was not cautioned in the No Risk condition. Trent & Ahmed (2013) have shown that weaker adaptation and weaker error sensitivity in response to errors further from the penalty region. This suggests that non-linear adaptation is an effective motor control strategy for avoiding penalty. In this study, larger compensation was observed in response to errors that were recognized as misses. This suggests that the larger compensation strategy is an effective control heuristic for avoiding consecutive misses. This tendency was robust regardless of the location of the penalty region. Thus, the results support the view that compensation on the following trial is influenced not only by the magnitude of the error but also by the subjective value of the error.

Several limitations should be discussed. In this study, I compared the observed mean response time calculated over 100 trials with the optimal mean response time in the $\mathrm{Risk}_{\mathrm{after}}/\mathrm{Risk}_{\mathrm{before}}$ condition and in each participant. Taking into account the fact that the location of the optimal mean response times move further from the reference time as response variance increases, the observed mean response times were closer than optimal to the reference time in both conditions (Figure 4A&B). However, a possibility remains that this observed response time would have approached optimal if the participants had been able to decrease their response variance through more practice. Therefore, the remaining issue is to investigate this possibility with a longitudinal study.

As another limitation, I instructed the participants to maximize the total gain but I did not use an experimental procedure giving them real monetary rewards in accordance with their performance. This raises the possibility that real monetary rewards would have induced risk-neutral behavior. However, it has been shown that real and virtual rewards induced similar performance in economic decision making (Bowman & Turnbull, 2003), autonomic response (skin conductance response) patterns resulted from monetary wins or loses (Carter & Pasqualini, 2004), and brain activation patterns (Miyapuram et al., 2012). Therefore, I consider that use of real monetary rewards would have a small effect on the participant's risk-seeking behavior. However, it would be interesting to investigate motor decision making in situations in which a one-trial decision wins a high-priced award, such as a game-winning shot or a tour-winning putt.

2-5. Supplementary information

2-5-1. Probability distribution of executed response time

In Equation 2-5 the model assumes that the probability distribution of an executed response time for given a planned response time follows a Gaussian distribution. To confirm that participant's response time is distributed according to a Gaussian distribution, I conducted Kolmogorov-Smirnov tests. As shown in Supplementary Table 2-1, the null hypothesis that response time follows a Gaussian distribution was not significantly rejected for 89.2 % (33/37) of participants in the No Risk condition, for 100 % (16/16) in the $\text{Risk}_{\text{after}}$ condition, for 100 % (12/12) in the $\text{Risk}_{\text{before}}$ condition, and for 88.8 % (8/9) in the Step condition. Thus, I conclude that response time t follows a Gaussian distribution.

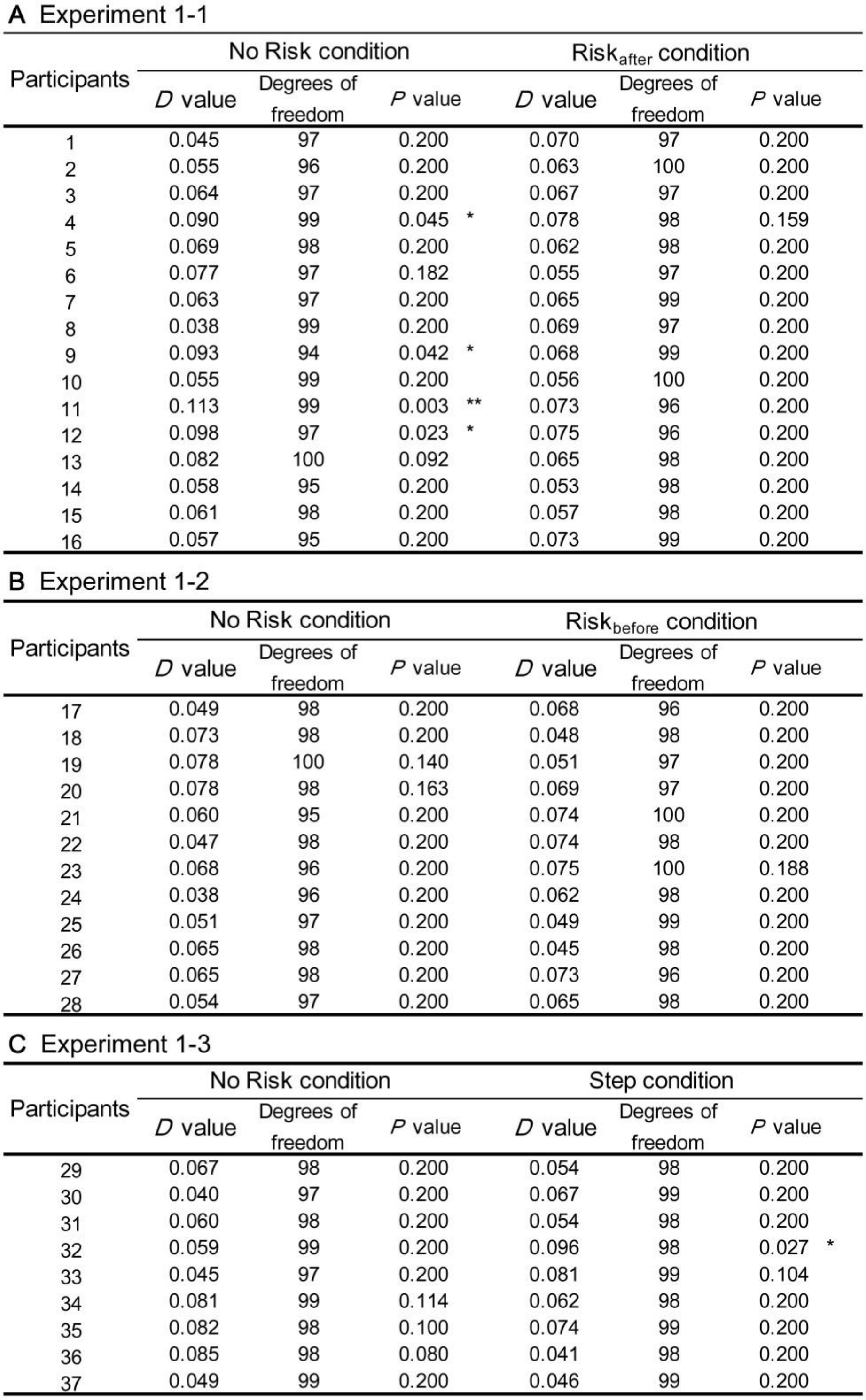
2-5-2. Magnitude of response error

I found that compensation in response to errors following miss trials was larger than that of following success trials (Figure 6). However, compensation size $(RT_{n+1} - RT_n)$ should be calculated differently between conditions if the magnitude of response error on the current trial (E_n) were different in each bin. To assess this possibility, I compared response error on the current trial in the $\text{Risk}_{\text{after}}$/$\text{Risk}_{\text{before}}$ condition with that in the No Risk condition across bins. Mean response error across participants on the current trial is shown in Experiment 1 in Supplementary Figure 2A and in Experiment 2 in Supplementary Figure 2B. First, I performed two-way repeated-measures ANOVA on the response error in Experiment 2. The levels were condition (2: $\text{Risk}_{\text{before}}$ condition and No Risk condition) and bin (4: bin1-4). I found no main effect of condition (F [1, 11] = 1.76, p = 0.21) or interaction effect (F [3, 33] = 0.27, p = 0.85). Therefore, I conclude that the magnitude of the response error in the $\text{Risk}_{\text{before}}$ condition was not significantly different from that in the No Risk condition for any bin (Supplementary Figure 1B). I also performed two-way repeated-measures ANOVA on the response error in Experiment 1. The levels were condition (2: $\text{Risk}_{\text{after}}$ condition and No Risk condition) and bin (4: bin1-4). Although I found no main effect of condition (*F* [1, 15] = 0.00, *p* = 0.99), I found an interaction effect (*F* [2.15, 32.22] = 4.69, *p* < .05). The simple main effect revealed that the mean response error across participants in the $\text{Risk}_{\text{after}}$ condition was significantly smaller than that in the No Risk condition only in bin 1 (*F* [1, 15] = 5.02, *p* < .05). There was no difference between conditions in bins 2, 3, or 4 (*Fs* [1, 15] < 4.32, *ps* > .05). From these results, compensation size was calculated assuming uniform magnitudes of response error except for the case of bin 1 in Experiment 1.

Although in this bin mean response error was different between conditions, I assume that this result would have a small influence on our results on compensation size for the following reason. I focused on the compensation size following miss trials (bin 4 in Experiment 1). Mean response error was not different between conditions in this bin. Thus, a difference in the magnitude of response errors in bin 1 does not cause the observed larger compensation following miss trials.

Supplementary Table 2-1. The results of Kolmogorov-Smirnov test.

The results show that the null hypothesis that the response time follows a Gaussian distribution was not rejected for almost all of the participants. * indicates p < .05, ** indicates p < .01, and *** indicates p < .001.



A Experiment 1-1

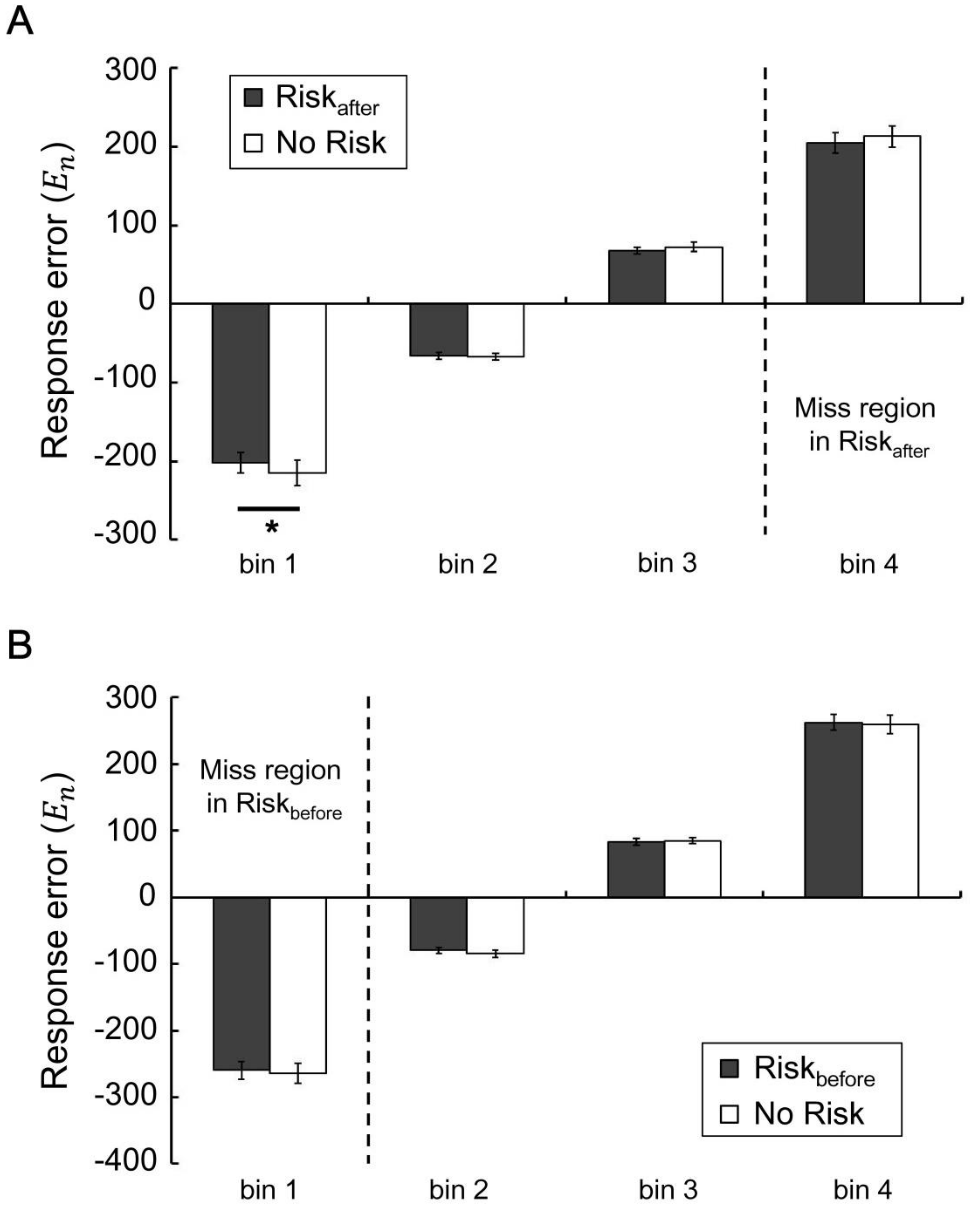
Participants	No Risk condition			Risk$_{after}$ condition		
	D value	Degrees of freedom	*P* value	*D* value	Degrees of freedom	*P* value
1	0.045	97	0.200	0.070	97	0.200
2	0.055	96	0.200	0.063	100	0.200
3	0.064	97	0.200	0.067	97	0.200
4	0.090	99	0.045 *	0.078	98	0.159
5	0.069	98	0.200	0.062	98	0.200
6	0.077	97	0.182	0.055	97	0.200
7	0.063	97	0.200	0.065	99	0.200
8	0.038	99	0.200	0.069	97	0.200
9	0.093	94	0.042 *	0.068	99	0.200
10	0.055	99	0.200	0.056	100	0.200
11	0.113	99	0.003 **	0.073	96	0.200
12	0.098	97	0.023 *	0.075	96	0.200
13	0.082	100	0.092	0.065	98	0.200
14	0.058	95	0.200	0.053	98	0.200
15	0.061	98	0.200	0.057	98	0.200
16	0.057	95	0.200	0.073	99	0.200

B Experiment 1-2

Participants	No Risk condition			Risk$_{before}$ condition		
	D value	Degrees of freedom	*P* value	*D* value	Degrees of freedom	*P* value
17	0.049	98	0.200	0.068	96	0.200
18	0.073	98	0.200	0.048	98	0.200
19	0.078	100	0.140	0.051	97	0.200
20	0.078	98	0.163	0.069	97	0.200
21	0.060	95	0.200	0.074	100	0.200
22	0.047	98	0.200	0.074	98	0.200
23	0.068	96	0.200	0.075	100	0.188
24	0.038	96	0.200	0.062	98	0.200
25	0.051	97	0.200	0.049	99	0.200
26	0.065	98	0.200	0.045	98	0.200
27	0.065	98	0.200	0.073	96	0.200
28	0.054	97	0.200	0.065	98	0.200

C Experiment 1-3

Participants	No Risk condition			Step condition		
	D value	Degrees of freedom	*P* value	*D* value	Degrees of freedom	*P* value
29	0.067	98	0.200	0.054	98	0.200
30	0.040	97	0.200	0.067	99	0.200
31	0.060	98	0.200	0.054	98	0.200
32	0.059	99	0.200	0.096	98	0.027 *
33	0.045	97	0.200	0.081	99	0.104
34	0.081	99	0.114	0.062	98	0.200
35	0.082	98	0.100	0.074	99	0.200
36	0.085	98	0.080	0.041	98	0.200
37	0.049	99	0.200	0.046	99	0.200



Supplementary Figure 2-1. The difference in mean response error on current trial between conditions in Experiment 1 (A) and Experiment 2 (B). Mean response error on current trial across participants was plotted in each bin and condition. * indicates $p < .05$. Error bars indicate standard error of the mean.

Chapter 3.

Sub-optimality of spatial motor plan under an asymmetric gain function

A part of this study has been accepted as:

太田啓示・森岡祐平・進矢正宏・工藤和俊. (in press). リスク下におけるゴルフパッティング距離調整. *東京体育学研究*. 8.

3-1. Introduction

It is suggested that imaginary skills, managing psychic energy, stress management, attentional skills, and self-confidence and goal-setting skills are important for an athlete as psychological skills (Martens, 1987). In addition to these skills, it is considered that decision-making is important for the athlete. For example, a golf player requires a decision about where they aim. The golf player is sometimes faced with a situation in which there is a banker in a back of the green and a pin location is close to the banker (Figure 3-1). In this situation, the player can probably drop a ball in the cup in the following putt if a stroked ball stops near the cup, while the probability of falling in the banker also increases as he/she aims closer to the cup (Figure 3-1B). Thus, the player is faced with the situation in which higher gain comes with risk of zero gain or negative gain.

In Chapter 2, I demonstrated that decision-making in a coincident timing task can be risk-sensitive under such asymmetric gain function. However, it is unclear whether such behavior holds or not when other motor tasks are applied. In other words, there is the possibility that the suboptimal behavior depends on the motor task involving temporal action plan. Thus, the first purpose of this study is aimed to examine whether risk-sensitive decision-making is also confirmed in the motor task involving spatial action plan. The second purpose of this study is aimed to investigate whether humans can alter an aiming point taking motor output variability which depends on the magnitude of the executed motor plan into account. The noise in our motor control system is signal-dependent; larger control signals induce larger variability of motor output (Harris & Wolpert, 1998; Schmidt et al., 1979). This signal-dependent motor output variability affects a motor plan. Considering the situation stated above, the player can perform less variable shot when the approach distance to the cup is short (Figure 3-1A), and thus it would be better to aim close to the cup. In contrast, the shot variability increases when the distance is long, and then the ball would fall in the banker if the player aims at the same point as the short distance (Figure 3-1B). Therefore, the player should switch the aiming point with the distance of approach even in the same situation.

To address the two questions stated above, I exploited a golf putting task and prepared two (2 m and 3 m) conditions for putt distance. In this study, I first demonstrate that risk-sensitive decision-making found in a coincident timing task is also confirmed in a golf putting task. I then show that changes in motor output variability induced by put distances are not likely to alter an aiming point under risk.

3-2. Methods

3-2-1. Participants

Sixteen healthy right-handed adults (13 male, 3 female; mean age 22.4 ± 1.7 years) participated in Experiment 2. All participants have no golf experience and were unaware of the purpose of the experiment. This study was approved by the Ethics Committee of the Graduate School of Arts and Sciences, the University of Tokyo.

3-2-2. Experimental setup

I used a golf putting task in this study. Figure 3-2A shows the experimental setup. The putter mat (RG-350, UNITIKA), which size was 100 × 600 cm, was laid on the flat floor in an experimental room. The initial position for putting a ball was marked on 50 cm from the left end. The white line was marked on 2 m and 3 m from the initial position, as a reference line. The participants performed the putting task referring this white line with the same putter (USA PRO, Tommy Aaron).

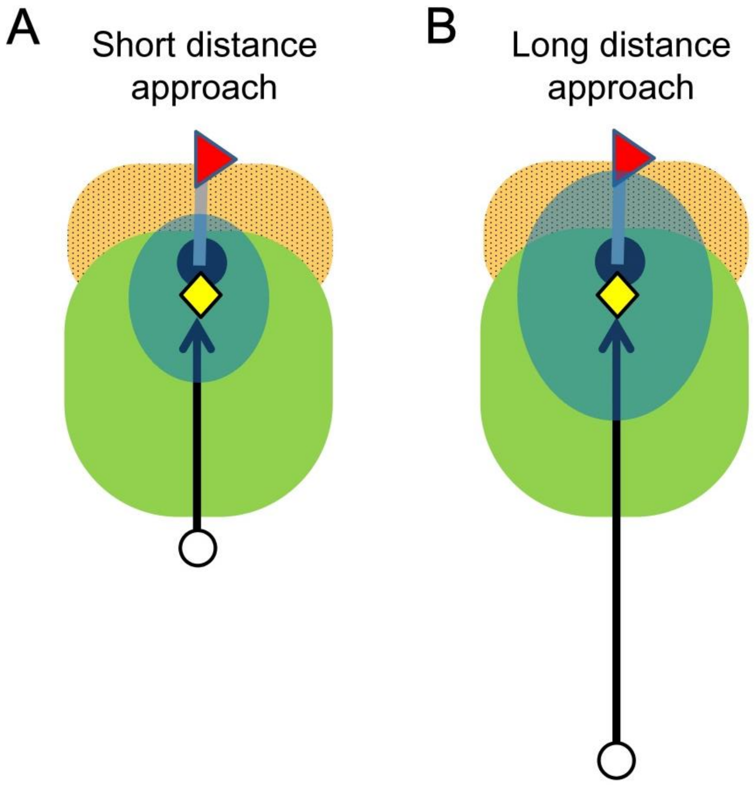


Figure 3-1. Schematic illustration of decision-making in golf.

The illustration shows the situation in which there is a banker in back of green. When approach distance is short (A), the variance of stroked ball position (shown as blue ellipse) is small. When approach distance is long (B), it can increase. Yellow diamond represents aiming point of shot.

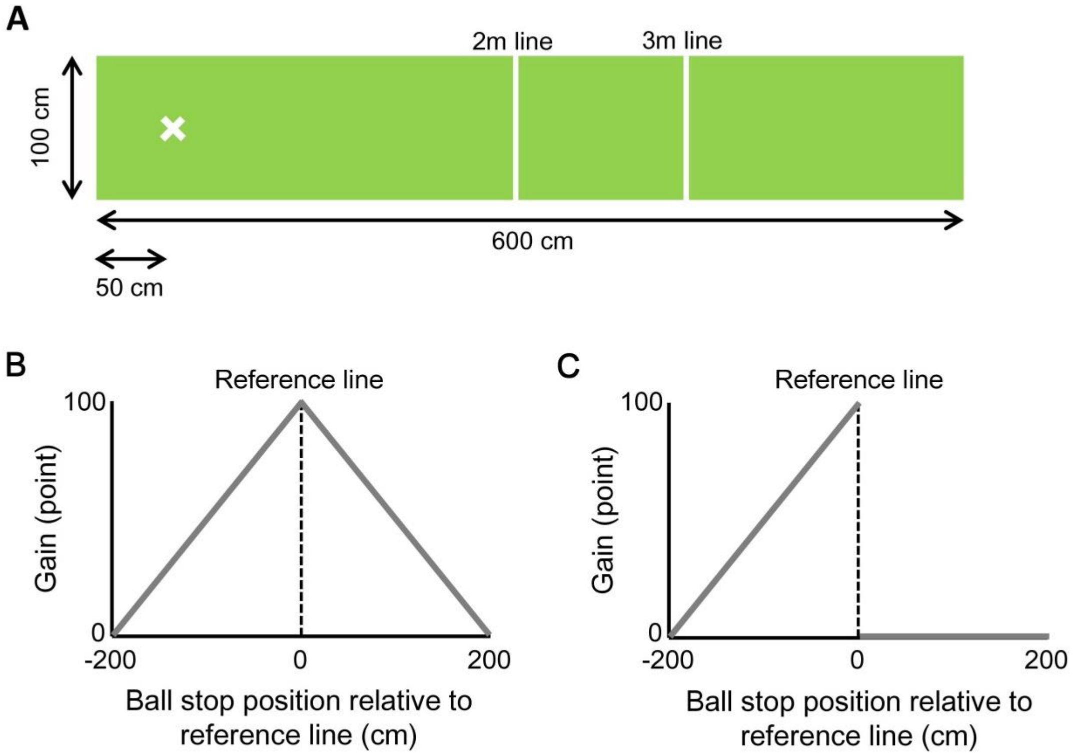


Figure 3-2. Experimental task and condition.

(A) Golf putting task. The participants putt a ball from an initial position (shown as white X) referring 2 m or 3 m line. (B) No Risk condition. (C) Risk condition. The gain per trial was determined by a symmetric (B) or an asymmetric (C) gain function as a function of ball stop position.

3-2-3. Experimental condition

Four experimental conditions were tested: 1) 2 m No Risk condition, 2) 2 m Risk condition, 3) 3 m No Risk condition, and 4) 3 m Risk condition. The No Risk condition (Figure 3-2B) employed an asymmetric gain function in which a gain G was proportional to the absolute value of the ball stop position p relative to the reference line as follows.

$$G(p) = \begin{cases} \frac{1}{2}p + 100, & if\ p \leqq 0 \\ -\frac{1}{2}p + 100, & if\ p > 0 \end{cases} \qquad (3\text{-}1)$$

Here I defined the ball stop position p (cm) as the difference between the reaching distance from the initial position and the reference line. The gain reduced by 0.5 points as the ball stop position deviated by 1 cm from the reference line. Therefore, gains can be obtained if the ball stops the location from 1 cm to 399 cm in 2 m No Risk condition and from 101 cm to 499 cm in 3 m No Risk condition, relative to the initial position.

The Risk condition (Figure 3-2C) had an asymmetric gain function in which the gain was proportional to the stop position relative to reference line if the ball stopped on the reference line or below the reference line. However, no gain was attributed if the ball stopped over the reference line. The gain was determined by the following equation.

$$G(p) = \begin{cases} \frac{1}{2}p + 100, & if\ p \leqq 0 \\ 0, & if\ p > 0 \end{cases} \qquad (3\text{-}2)$$

Therefore, gains can be obtained if the ball stops the location from 1 cm to 200 cm in 2 m No Risk condition and from 101 cm to 300 cm in 3 m No Risk condition, relative to the initial position.

3-2-4. Experimental procedure

In each trial, feedback information consisting of ball stop position relative to the reference line and gain for the trial were provided to the participants. The ball position was measured with a spatial resolution of 1 cm. For practice, the participants firstly putt a ball aiming at 2 m reference line for 10 trials and then putt a ball aiming at 3 m reference line for 10 trials. After the practice, they performed four experimental conditions for 30 trials, respectively. The order of the experimental condition was balanced across participants, and they were randomly assigned to one of the following order: 1) 2m No Risk condition → 2 m Risk condition → 3 m No Risk condition → 3 m Risk condition, 2) 2m Risk condition → 2 m No Risk condition → 3 m Risk condition → 3 m No Risk condition, 3) 3 m No Risk condition → 3 m Risk condition → 2m No Risk condition → 2 m Risk condition, and 4) 3 m Risk condition → 3 m No Risk condition → 2m Risk condition → 2 m No Risk condition. The participants were instructed to maximize the total gain for 30 trials in each experimental condition as possible as they could.

3-2-5. Model assumptions

Similar to the Bayesian model used in Chapter 2, I calculated the expected gain as a function of planned ball stop position P by integrating the gain function $G(p)$ in the Risk condition over the probability distribution of observed stop position $P(p|P)$ as follows.

$$EG(P) = \int_{-\infty}^{\infty} G(p) \cdot P(p|P) dp \qquad (3\text{-}3)$$

$$P(p|P) = \frac{1}{\sqrt{2\pi\sigma^2}} exp\left[-\frac{(p-P)^2}{2\sigma^2}\right] \qquad (3\text{-}4)$$

For given participant's variance of stop position σ, I calculated the optimal mean ball stop position by maximizing Equation 3-3 and then compared the observed mean ball stop position.

3-2-6. Data analysis

Trials with ball stop potions more than ±2.5 standard deviations from the mean were excluded from the analysis as outliers. The average number of trials excluded across participants was 0.2 ± 0.4 trials for 2 m No Risk condition, 0.4 ± 0.6 trials for 2 m Risk condition, 0.2 ± 0.4 trials for 3 m No Risk condition, and 0.1 ± 0.3 trials for 3 m Risk condition.

3-3. Results

Figure 3-3 shows a profile of ball stop position relative to the reference line for a participant. Each circle represents each ball stop position and a diamond represents the mean stop position. The mean stop position in No Risk conditions locates on or close to the reference line, whereas that in Risk conditions locates below the reference line. There is no large difference between the mean stop position in 2 m Risk condition and that in 3 m Risk condition.

I first analyzed whether a suboptimal motor plan found in a coincident timing task is also confirmed in a golf putting task. Similar to Chapter 2, the observed mean ball stop positions were plotted against the SD of stop positions in Risk conditions for all participants (Figure 3-4). The optimal mean stop position calculated by Bayesian model and its 95 % confidence interval (CI) were also plotted. The observed mean stop position was closer to the reference line than 95 % CI of the optimal mean stop position for eight of sixteen participants in 2 m Risk condition (Figure 3-4A) and ten of sixteen participants in 3 m Risk condition (Figure 3-4B). In contrast, it was further from the reference line than the 95 % CI of the Bayesian model for two of sixteen participants in 2 m Risk condition and one of sixteen participants in 3 m Risk condition. Therefore, ten of sixteen in 2 m Risk condition and eleven of sixteen in 3 m Risk condition took higher or lower risk than optimal risks given their own motor output variability. Overall, in Risk conditions, the observed mean stop positions were significantly shorter than the optimal mean stop positions, relative to the reference lines (2m Risk: t [15] = 2.68, $p < 0.05$, d =

0.92, 3 m Risk: t [15] = 4.65, $p < 0.001$, $d = 1.66$). These results suggest that the sub-optimal behavior found in a coincident timing task is also confirmed in a golf putting task involving risks.

I then tested whether the participants altered their motor plan with the increase/decrease of motor output variability. To this end, I first performed two-way (gain function [2: No Risk and Risk] × distance [2: 2m and 3m]) repeated measures ANOVA to determine the difference in the variability of the ball stop position among conditions. As a result, I found the main effect of distance (F [1, 15] = 105.57, $p < 0.001$, η^2 = 0.80) and the interaction effect (F [1, 15] =6.97, $p < 0.05$, η^2 = 0.01). Simple main effect test revealed that there was the simple main effect of distance in No Risk condition (F [1, 15] = 77.35, $p < 0.001$, η^2 = 0.84) and Risk condition (F [1, 15] = 107.77, $p < 0.001$, η^2 = 0.88). Therefore, the SD of ball stop position in 3 m Risk condition was significantly larger than that in 2 m Risk condition ($p < 0.001$, Figure 3-5A) and the SD of ball stop position in 3 m No Risk condition was significantly larger than that in 2 m No Risk condition ($p < 0.001$, Figure 3-5A). The 3mRisk-to-2mRisk ratio of motor output variability was 1.63.

I next performed two-way repeated measures ANOVA to determine the difference in the mean ball stop position among conditions. The result showed that there was the main effect of gain function (F [1, 15] = 77.86, $p < 0.001$, η^2 = 0.84) but there was neither the main effect of distance (F [1, 15] = 2.32, $p = 0.15$, η^2 = 0.01) nor the interaction effect (F [1, 15] = 0.21, $p = 0.66$, η^2 = 0.00). The simple main effect of gain function was observed in 2 m condition (F [1, 15] = 77.88, $p < 0.001$, η^2 = 0.84) and 3 m condition (F [1, 15] = 59.06, $p < 0.001$, η^2 = 0.80) but the simple main effect of distance was not observed either in No Risk condition (F [1, 15] = 2.06, $p = 0.17$, η^2 = 0.12) or in Risk condition (F [1, 15] = 1.74, $p = 0.21$, η^2 = 0.10). Therefore, as shown in Figure 3-5B, the observed mean stop position in 2m Risk condition was significantly smaller than that in 2m No Risk condition ($p < 0.001$) and the observed mean stop position in 3 m Risk condition was significantly smaller than 3 m No Risk condition ($p < 0.001$). However, there was no significant difference either between 2 m No Risk condition and 3 m No Risk condition or between 2 m Risk condition and 3 m Risk condition. These results suggest that participants performed the putting task aiming at or close to the reference line in No Risk condition and shifted the strategy toward short distance in Risk condition. However, compared to this difference, they did not alter the aiming point between 2 m Risk condition and 3 m Risk condition. In 3 m Risk condition in which motor output variability is large, the strategy aiming at the same point as 2 m Risk condition results in increasing the number of miss trials, as illustrated in Figure 3-1. Actually, the number of miss trials in 3 m Risk condition is marginally significantly larger than that in 2 m Risk condition (2m Risk: 4.2 ± 2.7 trials, 3 m Risk: 5.6 ± 3.0 trials, t [15] = 1.82, $p = 0.090$).

The effect sizes of simple main effect test are summarized in Table 3-1. As shown in Table 3-1, in the SD of ball stop position, larger effect size was confirmed in the test between different distances (i.e., NR [2m vs 3m] or R [2m vs 3 m]) compared to the test between the same distances (i.e., 2m [NR vs R] or 3m [NR vs R]). In contrast, in the mean ball stop position, larger effect size was confirmed in the test between different gain functions (i.e., 2m [NR vs R] or 3m [NR vs R]) compared to the test between the same gain functions (i.e., NR [2m vs 3m] or R [2m vs 3 m]). Again, these results indicate that participants did not shift the putting distance between Risk conditions (2 m Risk v.s. 3m Risk), compared to the putting distance between No Risk condition and Risk condition.

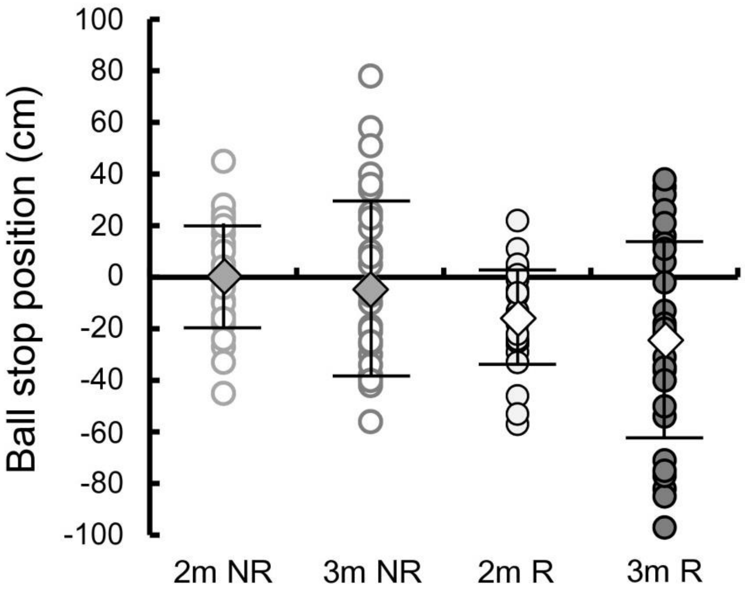


Figure 3-3. Distribution of ball stop position for a participant.

Each circle represents each ball stop position, a diamond represents mean stop position across all trials, and error bar represents standard deviation.

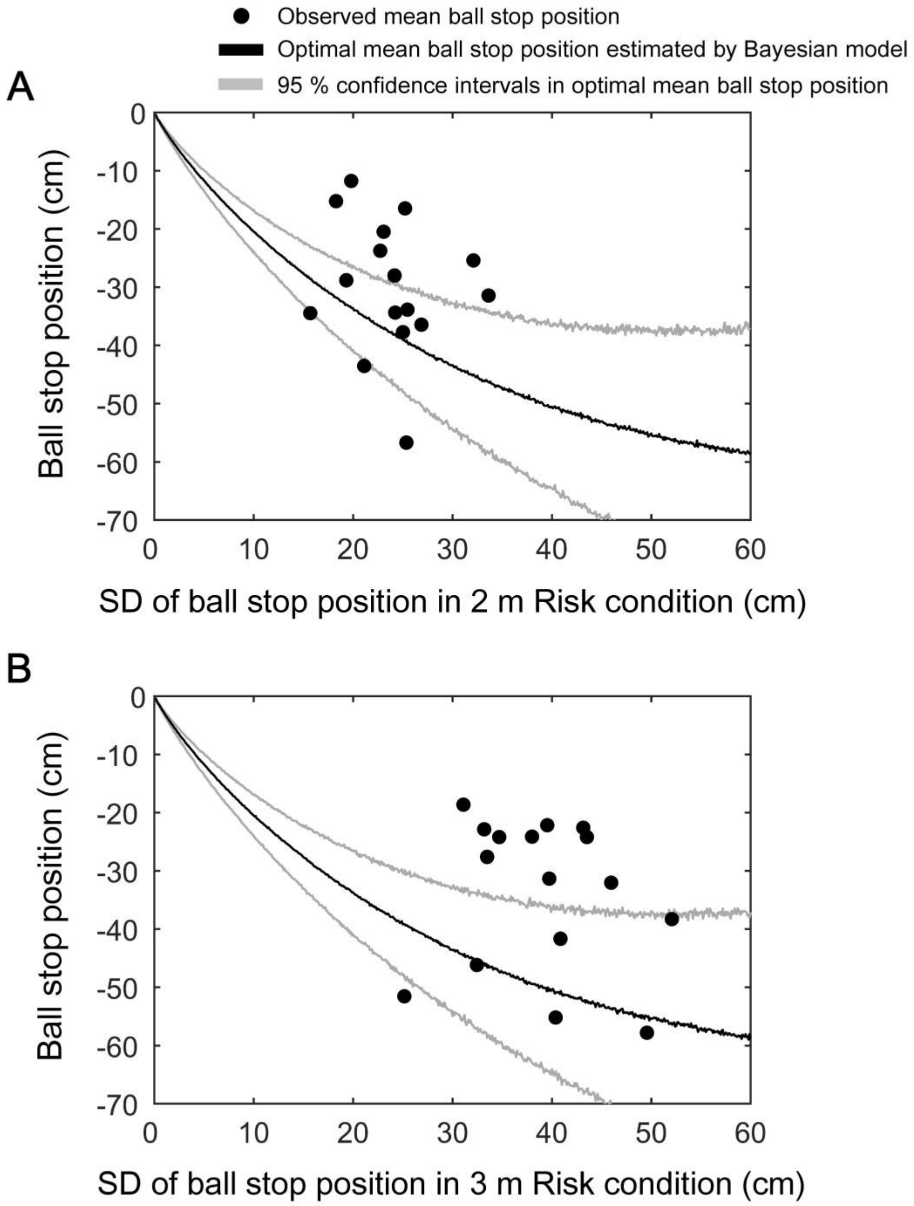


Figure 3-4. Comparison of the observed motor plan and the optimal motor plan. Half participants adopted risk-seeking strategy in 2 m Risk condition (A) and 3 m Risk condition (B). Note that 95 % confidence intervals (CI) in optimal mean ball stop position cover wider range than that in optimal mean response time, shown in Figure 2-5. This is because a bootstrap estimation for 95 % CI was conducted with 30 trials in a golf putting task and with 100 trials in a coincident timing task.

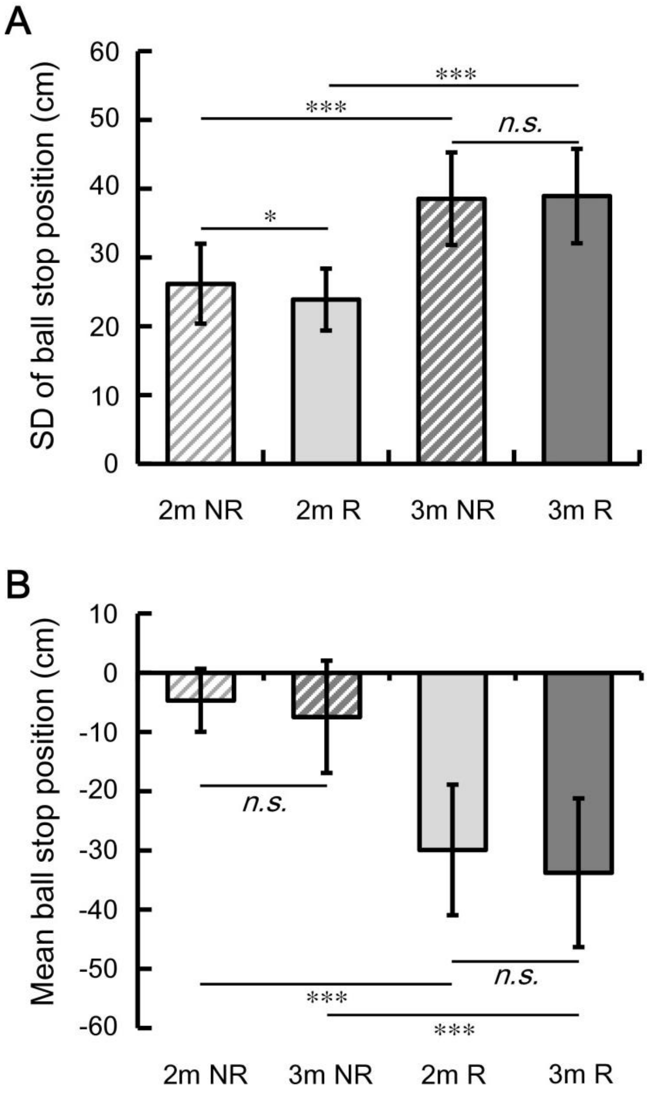


Figure 3-5. Statistical profile of ball stop position.

(A) SD of ball stop position increased in 3 m condition compared to 2 m condition. (B) However, mean ball stop position was not significantly different between 2 m Risk condition and 3 m Risk condition. These results suggest that participants did not alter their aiming point even through movement variability increased. * indicates $p < 0.05$ and *** indicates $p < 0.001$.

Table 3-1. Comparison of effect sizes in simple main effect test.

η^2 value		Simple main effect of distance		Simple main effect of gain function	
		NR (2m vs 3m)	R (2m vs 3m)	2m (NR vs R)	3m (NR vs R)
Ball stop position	SD	0.84	0.88	0.26	0.01
	Mean	0.12	0.1	0.84	0.8

3-4. Discussion

Chapter 3 investigated whether risk-sensitive decision-making found in Chapter 2 depends on the motor task involving temporal action plan or not. The results showed that ten or eleven of sixteen participants took suboptimal spatial action plan in a golf putting task under Risk conditions. It suggests that risk-sensitive decision-making under an asymmetric gain function does not depend on a temporal task or a spatial task.

Chapter 3 then examined whether humans can alter an aiming point with changes in motor output variability. To address this question, I first confirmed that the SD of ball stop position in 3 m Risk condition was significantly larger than that in 2 m Risk condition. The motor output variance in 3 m Risk condition was 1.63 times larger than that in 2 m Risk condition. Thus, it was confirmed that the noise in putting movement is signal dependent in line with previous studies (Harris & Wolpert, 1998; Schmidt et al., 1979). Since the optimal aiming point under risk depends on motor output variability, the aiming point should be changed with increase/decrease of motor output variability. However, there was no significant difference between the mean ball stop position in 2 m Risk condition and that in 3 m Risk condition. It indicates that participants are not likely to alter their aiming point with the putting distance between Risk conditions. In contrast, the participants switched the aiming point from the close distance to the reference line in No Risk conditions, to the short distance from the reference line in Risk conditions. Therefore, these results suggest that they shifted the motor plan when the risk of zero gain was applied but they did not largely shift it when the motor output variability changed under risk. Again, such strategy results in increasing numbers of miss trials, as illustrated in Figure 3-1.

It is explicitly shown that the risk of zero gain is applied. In contrast, it is not explicitly shown that motor output variability increases or decreases and it is implicit in the motor system.

The previous study showed that participants appropriately shifted their aiming point compensating for changes in motor output variability by externally added perturbation (Trommershäuser et al., 2005). Furthermore, the previous studies suggest that human's representation of own motor error can be inaccurate, showing isotropic bias of own motor error (Zhang et al., 2013; Zhang, Kulsa, & Maloney, 2015). Therefore, it might be difficult to estimate internal changes in own motor output variability induced by signal-dependent-noise, especially for novice golf players. For future direction, it would be valuable to conduct the same experiment for experienced golf players who have more accurate knowledge about own putting error than the novice players. It is possible that they can alter the aiming point with changes in putting variability under risk. Moreover, studies to investigate the relationship among movement experience, cognition for own movement error, and the risk-handling strategy would give further findings on this issue.

Chapter 4.

Effect of learning on suboptimal motor plan through 9 days practice

This study has been published as:

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4-1. Introduction

In Chapter 2 and 3, it is suggested that motor decision making can be sub-optimal under an asymmetric gain function in which higher gain goes hand in hand with risk of zero gain. This tendency was held if either temporal or spatial motor plan was required, which suggests that it is difficult to make an optimal motor plan for maximizing the expected gain.

However, it is possible that this sub-optimal motor plan can be improved by repeated practice. In other words, it is not clear whether humans could learn to aim optimally by observing the results of their own motor output repeatedly, and accumulating knowledge about their own output distribution (motor variance). Although it is assumed that the practice reduces motor output variability (Kudo et al., 2000; Kudo & Ohtsuki, 2008; Lee & Carnahan, 1990; Lee et al., 1997; Shea & Kohl, 1991; Sherwood, 1988), how risk-seeking or risk-averse planners update their aiming point with a decrease in variability through repetitive practice is also unclear.

To address these questions, Chapter 4 designed a coincident timing task that required participant motor planning about when to respond under risk, and conducted a learning experiment that lasted 9 days. By showing that suboptimal motor planning was preserved throughout the 9 days of practice, Chapter 4 demonstrate that it is difficult to learn the optimal aiming point by repetition and that risk-preference is retained throughout the practice period.

4-2. Methods

4-2-1. Participants

This study was approved by the Ethics Committee of the Graduate School of Arts and Sciences, the University of Tokyo, and the methods were carried out in accordance with the approved guidelines. All the participants signed informed consent. Fifteen healthy right-handed adults (12 male, 3 female; mean age: 21.3 ± 3.9 years) participated in the Experiment 3. All the participants were unaware of the purpose of the experiment.

4-2-2. Experimental task and procedure

The experiment was conducted based on the task used in Chapter 2. The participants performed a coincident timing task under risk conditions. Figure 4-1A shows the time sequence of the basic experimental task. After a warning tone was sounded as the “ready” signal and a visual cue was given as the start signal, the participants pressed a button (Figure 4-1A). In each trial, they were told their relative response time (response time – reference time [fixed to 2300 ms]), the single trial gain, which was determined using the gain function, and the cumulative total gain as performance feedback. (In this study, I termed the average relative response time across trials the “mean response time”).The participants mainly performed the task under the Risk condition, which employed an asymmetric configuration of the gain function (Figure 4-1C). In this condition, higher gain (100 points at maximum) was attributed when the participants pressed a button with a response time that was closer to the reference time, whereas no gain (0 points) was attributed when their response time exceeded the reference time. When the participants failed to gain a point, they were cautioned by an unpleasant alarm that was sounded through their headphones (MDR-Z150, SONY, Tokyo, Japan) and a flashing red lamp on the screen. The volume of the alarm was 68.1 ± 0.8 dB. I defined these eventualities as a miss trial and any other trials as successful trials. The participants were required to make a decision about when to respond for maximizing the total gain in each block (1 block consisted of 50 trials) as best they could, and performed the task under the Risk condition for 5 blocks per day (45 blocks, or 2250 trials in total). I did not use actual monetary rewards/penalties; as I described in discussion of Chapter 2, small amounts of monetary rewards/penalties appear to have less influence on motor planning.

4-2-3. Model assumptions

4-2-3-1. Modeling of optimal motor plan

Based on the statistical/Bayesian decision theoretical approach (Hudson et al., 2012; O’Brien & Ahmed, 2013; Ota et al., 2015; Trommershäuser et al., 2003a, 2003b, 2005, 2008; Wu et al., 2006), I estimated the optimal mean response time in each experimental block by integrating the gain function $G(t)$ over the probability distribution of the executed response time $P(t|T)$ and compared it with participant’s actual mean response time. T represents possible response strategy (motor planning) and t represents the executed relative response time (motor output). The probability distribution of the executed response time followed a Gaussian distribution for a given planned response time and response variance as follows; this function is described in Figure 4-2A & 2B (left panels).

$$P(t|T) = \frac{1}{\sqrt{2\pi\sigma^2}} exp\left[-\frac{(t-T)^2}{2\sigma^2}\right] \qquad (4\text{-}1)$$

Given the particular magnitude of the response variance, I could calculate the expected gain as a function of the planned response time as follows; this function is also described in Figure 4-2A & 2B (middle panels).

$$EG(T) = \int_{-\infty}^{\infty} G(t) \cdot P(t|T)dt \qquad (4\text{-}2)$$

I defined the optimal mean response time for maximizing the expected gain (Figure 4-2A & 2B, middle panel), as follows.

$$T_{opt} = \underset{T}{\operatorname{argmax}}\, EG(T) \qquad (4\text{-}3)$$

Under the Risk condition, the optimal mean response time is located closer to the reference time, as the response variance is smaller (Figure 4-2C). If the observed mean response time T_{obs} (described in Figure 4-2A & 2B, right panels) corresponded to the optimal mean response time, it indicated a risk-neutral strategy for a given response variance. On the other hand, if it were located closer to or further from the reference time than the optimal value, the participant was adopting suboptimal risk-seeking (Figure 4-2A, right panel) or risk-averse strategies (Figure 4-2B, right panel). As an index of the optimality of motor planning, I calculated the difference between the observed mean response time T_{obs} and the optimal mean response time T_{opt}, as shown in Figure 4-2A & 2B, right panel, & Figure 4-2C.

Furthermore, I estimated the 95% confidence interval of the optimal mean response time using a bootstrap algorithm (visualized as gray curves in Figure 4-6). I simulated 50 trials of execution of a task within a certain optimal mean response time T_{opt}, with its response variance, 3000 times and obtained bootstrap samples. After I calculated the average of 1 sample in each bootstrap sample and sorted the 3000 average samples in ascending order, I defined a 2.5% and 97.5% point in the average samples as the 95% confidence interval within that optimal mean response time. Therefore, the way to improve the expected gain was to reduce the response variance and to learn the optimal motor plan for one’s own magnitude of response variance.

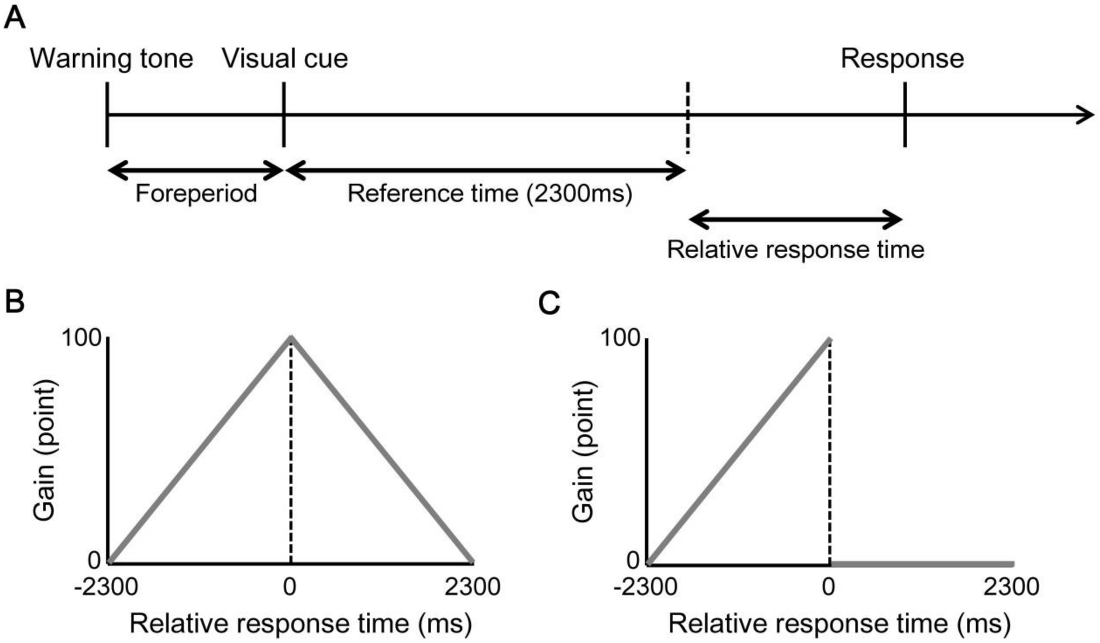


Figure 4-1. Experimental task and conditions.

(A) The coincident timing task. After a warning tone and a random foreperiod interval, a visual cue was presented as a starting signal. The participant was required to press a button. For each trial, the participants were rewarded with a point that was determined as a gain function of the relative response time. (B) No Risk condition. The gain was proportional to the absolute value of the relative response time. (C) Risk condition. The gain was proportional to the relative response time if the participants pressed a button equal to or before the reference time, whereas no gain was obtained if the response time exceeded the reference time.

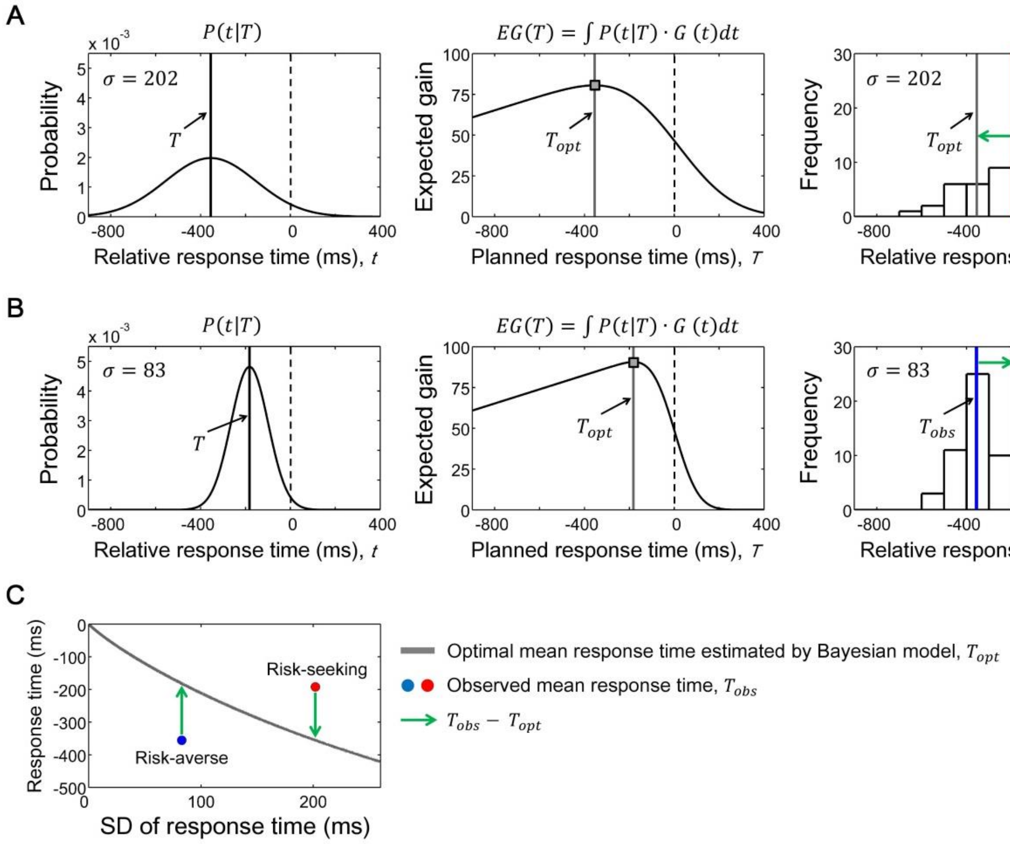


Figure 4-2. Modelling of the optimal motor plan.

(A) The optimal strategy in the case of large response variance ($\boldsymbol{\sigma = 202}$). The left panel shows the probability distribution of the executed response time. The solid black line indicates the planned response time in the probability distribution. The middle panel shows the expected gain as a function of the planned response time. The optimal mean response time $\boldsymbol{T_{opt}}$ was defined so as to maximize the expected gain (shown as a solid gray line). The right panel shows the actual histogram of the executed response time from a single participant. The observed mean response time $\boldsymbol{T_{obs}}$ (shown as a solid red line) is closer to the reference time than the optimal response time $\boldsymbol{T_{opt}}$; therefore, this strategy is classified as risk-seeking, as it leads to too many miss trials, shown in the filled bars. A 1-way green arrow shows the difference between $\boldsymbol{T_{obs}}$ and $\boldsymbol{T_{opt}}$. (B) The optimal strategy in the case of small response variance ($\boldsymbol{\sigma = 83}$). The middle panel shows that the optimal mean response time in the case of small variance is closer to the reference time than that in the case of large variance. The right panel also shows the actual histogram from a single participant In this case, the observed mean response time (shown as a solid blue line) is further from the reference time than the optimal time; therefore, this strategy is classified as a risk-averse strategy. (C) The panel shows that the optimal strategy depends on response variance. The optimal mean response time (shown as a gray curve) is located closer to the reference time, as the SD of the response time is smaller. If the observed mean response time was located in line with this curve, it could be proposed that participants behaved optimally given their own response variance. This example shows that the risk-seeking and risk-avoiding participants took higher (shown as a red circle) or lower (shown as a blue circle) than optimal risks, respectively.

4-2-3-2. Modeling of participant's utility function

I also explained the participant's suboptimal risk-sensitive behavior by introducing the utility function. Similar to the model used by O'Brien & Ahmed (2013), I calculated the expected utility $EU(T)$ as a function of the planned response time T, as follows.

$$EU(T) = G_i^{\alpha} \cdot P(R_j|T, \sigma^2) \qquad (4\text{-}4)$$

In this model, G_i^{α} represents the subjective gain. $P(R_j|T, \sigma^2)$ represents the probability that the executed response time falls in the reward region ($R_{reward}: -2300 < t \leq 0$) or the penalty region ($R_{penalty}: 0 < t \leq 2300$), for the given planned response time and response variance. The exponential parameter α represents participant's risk-sensitivity. A specific point reward G_i was defined by the following equation.

$$Gi = \begin{cases} 100 + \frac{T}{23}, & if\ -2300 < T \leq 0 \\ 0, & if\ \ 0 < T \leq 2300 \end{cases} \qquad (4\text{-}5)$$

The subjective optimal mean response time was calculated by maximizing Equation (4-4). I estimated the value of α for each day by fitting the observed mean response time data in 5 blocks to the model prediction. I used the *fminsearch* function in MATLAB to find α that minimized the mean squared error between them. To verify that we had searched for the global minimum, I repeated the search process using different starting points.

4-2-4. Practice protocol

I conducted 5 experimental sessions per day. In each experimental session, the participants firstly performed the task under the Risk condition for 1 block (50 trials). After the task, they then scored their current motivation, concentration, and sleepiness using a visual analogue scale (VAS). Lastly, they took 2–3 min rest to minimize fatigue. They moved to the next experimental session after this rest. The participants repeated this experimental session for 5 times per day. In addition to the Risk condition, they performed the task under the No Risk condition for 2 blocks (100 trials each) on the first day and on the last day.

The participants practiced the task approximately 3 times a week for 3 consecutive weeks. The average inter-practice interval was 2.28 ± 0.21 days across the participants (1 day at minimum, 6 days at maximum). This variability of the inter-practice interval did not influence the individual learning rate. There was no significant correlation between the inter-practice interval and the difference between the expected gain in the Risk condition on day 1 and that on day 9 ($r = -0.21$, $p = 0.46$, $df = 15$).

The participants were required to make a decision about when to respond for maximizing the total gain in each block (1 block consisted of 50 trials) as best they could, and performed the task under the Risk condition for 5 blocks per day (45 blocks, or 2250 trials in total). I used a visual as well as a verbal explanation to inform the participants about the structure of the gain function, prior to performing the task.

4-2-5. Data analysis

For each trial, I recorded the response time (button press time – onset of a visual cue) and calculated the relative response time (response time – the reference time). I could not obtain the trials conducted for the first block on day 1 in the Risk condition for P1 and P8. Thus, I analyzed the remaining 44 blocks for these. Trials in which the response times exceeded ±2.5 SD from the mean were excluded from the analysis as outliers. This resulted in the removal of 510 of a total of 33650 trials (1.5%) in the Risk condition and 55 of a total of 3000 trials (1.8%) in the No Risk condition. $P < 0.05$ was regarded as indicating statistical significance. Cohen's d measure was calculated as an index of effect size.

4-3. Results

4-3-1. Effect of learning on response variance and motor planning

I first analyzed the improvement in performance indexes induced by practice. The expected gain earned by the participants significantly increased from day 1 to day 9 (t [14] = -5.78, $p < 0.001$, d = -1.49, Figure 4-3A). The SD of the response time as an index of response variance also decreased from day 1 to day 9 (t [14] = 9.12, $p < 0.001$, d = 1.82, Figure 4-3B). Therefore, I confirmed that the participants obtained a smaller response variance with practice, and this resulted in the increase of the observed gain per trial. On the first day of the practice, I investigated whether the absolute difference between the observed and the optimal mean response time differed from the risk-neutrality value (i.e., 0), by a 1-sample t-test, and found it to be significantly different (t [14] = 5.25, $p < 0.001$, Figure 4-3C). I also found that it was significantly different from 0 on the last day of practice (t [14] = 3.26, $p < 0.01$, Figure 4-3C). These results suggested that the participants showed suboptimal risk-sensitive behavior on day 1 and still did on day 9.

I next focused on a time series of the response variance and the difference between T_{obs} and T_{opt}. The averaged values on a day (5 blocks) for both indexes are plotted in Figure 4-3D & 3E for all the participants (thin black lines). The averaged value across the participants (thick gray line) is also plotted. Dunnett’s post-hoc test after one-way repeated measures ANOVA showed that there were significant differences in the SD of response time on days 1, 2, and 3, compared to that on day 9 (one-way ANOVA: F [8, 112] = 15.40, $p < 0.001$, Dunnett’s test: $ps < 0.05$, Figure 4-3D). Thus, the decrease in the SD of the response time peaked at day 4, and plateaued thereafter. This is a general tendency in motor learning: rapid learning occurs at the beginning of a practice, and it becomes more gradual later on (Schmidt & Lee, 1999). If the practice could improve the risk-sensitive behavior observed on day 1, the difference between the observed mean response time T_{obs} and the optimal mean response time T_{opt} would converge toward 0 (risk-neutrality). However, no such trends were found in each participant (thin black lines, Figure 4-3E). In general motor learning tasks in which the position of the target at which participants should aim is designated by experimenters, the large constant error (i.e., a difference between the target and a motor response) emerges in the initial trial. By observing this error, the motor response gradually converges toward the target, and the constant error undershoots or overshoots crossing 0 thereafter (Takahashi et al., 2003). However, in this task (requiring a motor plan for aiming point), the value of the difference between T_{obs} and T_{opt} remained positive (risk-seeking) or negative (risk-averse). This would be one feature of learning during the motor planning under risk. Overall, compared to the difference between T_{obs} and T_{opt} on day 9, I only found it to be significantly smaller than that on day 1 (one-way ANOVA: F [8, 112] = 7.11, $p < 0.001$, Dunnett's test: $p < 0.001$).

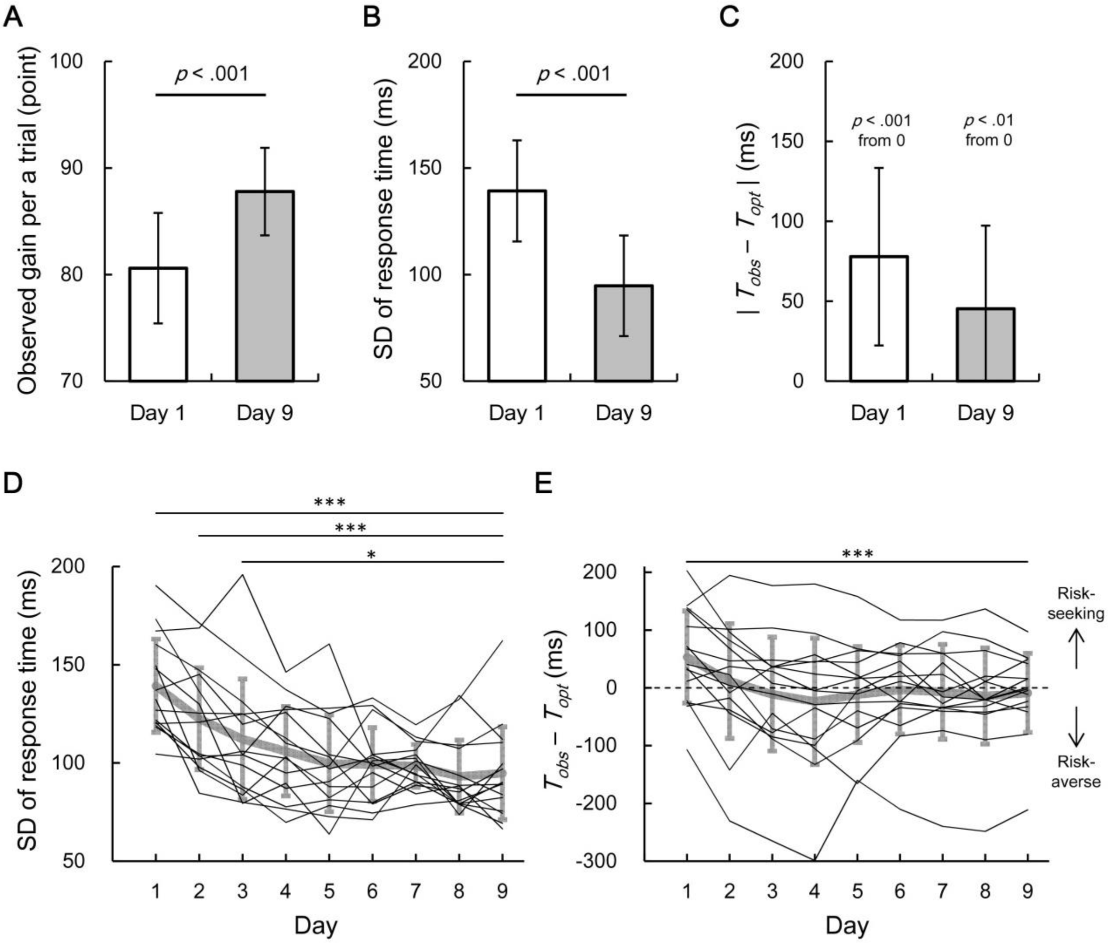


Figure 4-3. Effect of learning on performance indexes.

(A) Observed gain per trial. (B) Standard deviation (SD) of the response time. (C) Absolute difference between the observed mean response time T_{obs} and the optimal mean response time T_{opt}. The average value across the participants is plotted in each index, and the error bars indicate the standard deviation. (D & E) Time series of the SD of response time and the difference between T_{obs} and T_{opt}, shown for all the participants. The thin black lines represent the average value on a day (5 blocks) for each participant. Intra-personal errors are omitted for clarity. The thick gray line represents the average value across the participants and the error bars indicate the standard deviation. * indicates $p < 0.05$ and *** indicates $p < 0.001$, compared to day 9 (Dunnett's post-hoc test following one-way repeated measures ANOVA).

4-3-2. Consistency of motor planning under risk

Figure 4-4A shows the average difference between the observed and the optimal mean response time on day 1 against that on day 9 for all 15 participants. If the participants switched the strategy from risk-seeking to risk-averse and from risk-averse to risk-seeking, the slope of the regression line between day 1 and day 9 would be negative. If all the participants would take a risk-neutral strategy by day 9, the slope would be 0. A least-squares linear regression resulted in a slope of 0.70 (95% confidence interval of the slope: 0.41–0.998, $R^2 = 0.67$, $p < 0.001$), suggesting that the individual participants retained their risk-seeking or risk-averse strategies. This consistently held true when I performed the same linear regression analysis between other dates from day 1 to day 9 (Supplementary Table 4-1). The linear regression between other dates resulted in a mean slope of 0.81 ± 0.14.

On the last day of the practice, the observed gain per trial was significantly smaller than the optimal gain that the participants could theoretically obtain (t [14] = -2.69, $p < 0.05$, $d = -0.54$, Figure 4-4B). Thus, as shown in Figure 4-3C, the participants still showed suboptimal risk-sensitive behavior on day 9, and this yielded a reduced observed gain, as compared to the optimal gain. These findings suggest that the effect of learning on motor variability is effective, but it is difficult to learn the optimal motor plan for the given individual's motor variability, even over a practice period of 9 days.

Previous studies have confirmed risk-sensitive behavior in a motor task and have explained the reason from the basis of the prospect theory (O'Brien & Ahmed, 2013; Nagengast et al., 2011b; Wu et al., 2009) which proposed that individual risk-sensitivity can be explained by a distortion of utility function (Kahneman & Tversky, 1979). Here I explained the participant's behavior by introducing the utility function, similar to the study by O'Brien & Ahmed (2013). The utility of the reward (subjective reward) is represented by the power function of the actual reward (Lee, 2005), $U(x) = x^{\alpha}$. The participant's specific exponential parameter α represents their risk-sensitivity. In this study, the participants with a convex utility function ($\alpha > 1$) would likely respond closer to the reference time (risk-seeking behavior). In contrast, the participants with a concave utility function ($\alpha < 1$) would likely respond further from the reference time (risk-averse behavior). I estimated the value of α for each day and each participant by fitting the observed mean response time data in a day (5 blocks) to the subjective optimal mean response time that maximizes the expected utility.

In Figure 4-5A, the estimated value of α in each participant (thin black lines) against practice dates was plotted. A thick gray line represents the averaged value across the participants. Eleven of 15, nine of 15, and seven of 15 participants had a convex utility function on day 1, day 2, and day 9, respectively (mean α = 2.62 ± 2.04, 1.95 ± 1.71, and 1.41 ± 1.31). Dunnett's post-hoc test following one-way repeated measures ANOVA showed that there was the significant difference in α only on day 1, as compared to α on day 9 (one-way ANOVA: F [8, 112] = 2.99, $p < 0.05$, Dunnett's test: $p < 0.001$), suggesting that the change in the utility function reached a plateau at day 2. I next performed linear regression analysis. A least-squared linear regression between α on day 1 and α on day 9 resulted in a slope of 0.39 (95% confidence interval of the slope: 0.09–0.70, $R^2 = 0.37$, $p < 0.05$, Figure 4-5B). I performed the same regression analysis between other dates from day 1 to day 9. A linear regression resulted in a mean slope of 0.79 ± 0.19. The findings indicated that the participants showed a consistent trend in the direction of the distortion in the utility function (convex or concave function).

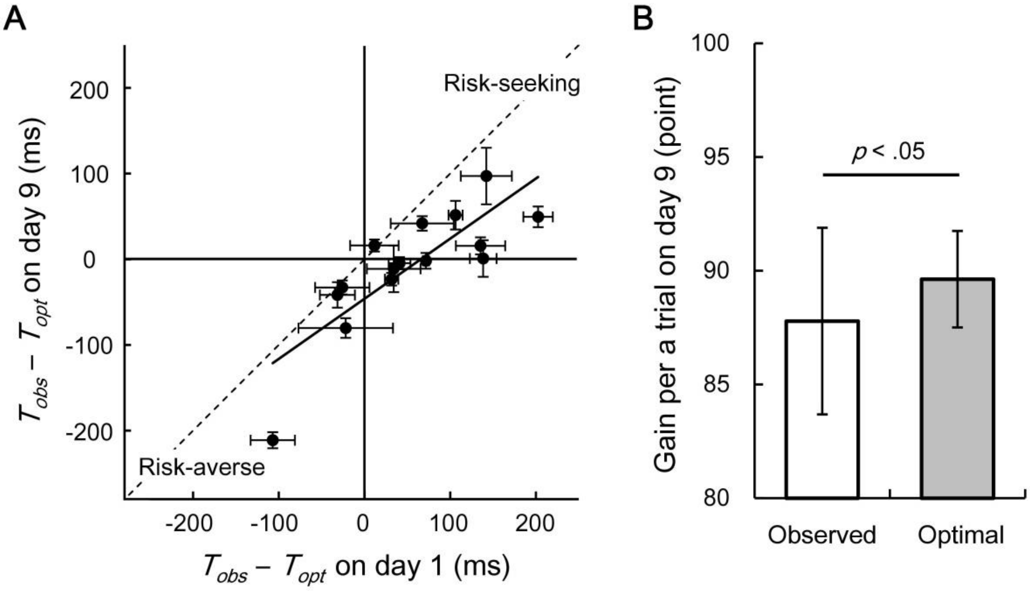


Figure 4-4. Suboptimal behavior was preserved after the practice.

(A) The average difference between the observed mean response time T_{obs} and the optimal mean response time T_{opt} on day 1 (5 blocks) is plotted against that on day 9 for all the participants. Horizontal and vertical error bars indicate the standard errors of the mean within day 1 and day 9, respectively. Data points that fall in the top right quadrant correspond to the risk-seeking to risk-seeking strategy. Data points that fall in the bottom left quadrant correspond to the risk-averse to the risk-averse strategy. (B) On day 9, there was a significant difference between the observed gain and the optimal gain per trial. The average value across the participants and the standard deviation is plotted.

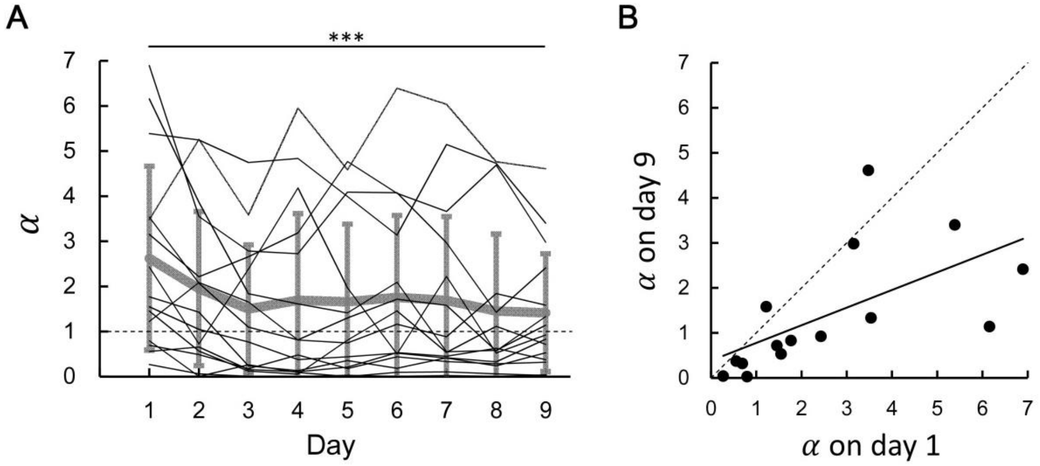


Figure 4-5. Estimation of the utility function.

(A) Time series of the estimated values of α. The thin black lines represent the value of α on a day for each participant. The thick gray line represents the average value across the participants and the error bars indicated the standard deviation. *** indicates $p < 0.001$ compared to day 9 (Dunnett's post-hoc test following one-way repeated measures ANOVA). (B) The value of α on day 1 is plotted against that on day 9. Each circle represents each participant.

4-3-3. Inter personal difference in the transition of the motor plan

I next showed the various transition patterns of the observed mean response time for participants with a different strategy. In Figure 4-6, I plotted the observed mean response times for all 45 blocks (circles), the optimal mean response time (black curve), and its 95% confidence intervals (gray curves) against the SD of the response time. As shown in Figure 4-6, the SD of the response time gradually decreased as the practice proceeded, while the observed mean response times were distributed differently. In participant P1 (risk-seeking), the observed mean response times were closer to the reference time than the upper limit of the 95% confidence interval (Figure 4-6, left panel). This participant consistently had a response time close to the reference time, regardless of the magnitude of the response variance. In contrast to P1, participant P4 (risk-averse) had response times that gradually became closer to the reference time, with a decrement in the response variance, but with the observed mean response times further from the reference time than the lower limit of the 95% confidence interval (Figure 4-6, right panel). These participants took lower or higher than optimal risks, given their own variance in motor output. For participant P2 (risk-neutral), the observed mean response times were mostly distributed within the Bayesian-theoretical 95% confidence interval (Figure 4-6, middle panel). This participant had response times that gradually approached the reference time, with a decrease in the response variance for taking optimal risks. Thus, there are different transition patterns in aiming for a given current motor variability. For the results of the other participants, see Figure 4-7.

To investigate the optimality of motor planning under a symmetric gain function, I also tested the No Risk condition, in which the gain was also achieved if the participants responded after the reference time, and it was proportional to the absolute value of the relative response time (Figure 4-1B). The participants performed this condition for 100 trials on day 1 and day 9.

Under the No Risk condition, it was confirmed that there were no significant differences (t [14] = 1.26, p = 0.23, d = 0.46) between the optimal (Mean = 0 ± 0 ms) and the observed mean response time on day 1 (Mean = 18.86 ± 57.92 ms). This result verified that the suboptimal motor planning found under the Risk condition was due to the asymmetric configuration of the gain function.

In Equations 4-1 and 4-2, I modelled the optimal mean response time based on the assumption that temporal variance is constant regardless of the magnitude of planned response time. According to Weber's law, the standard deviation (SD) of response time could be proportional to the magnitude of the planned response time (Jazayeri & Shadlen, 2010). Here I calculated the optimal mean response time based on the model that takes Weber's law into account. I found that there was a marginal difference between these two models, suggesting that the issue of Weber's law (signal-dependent noise) would not jeopardize my argument (for detail, see Supplementary Figure 4-1).

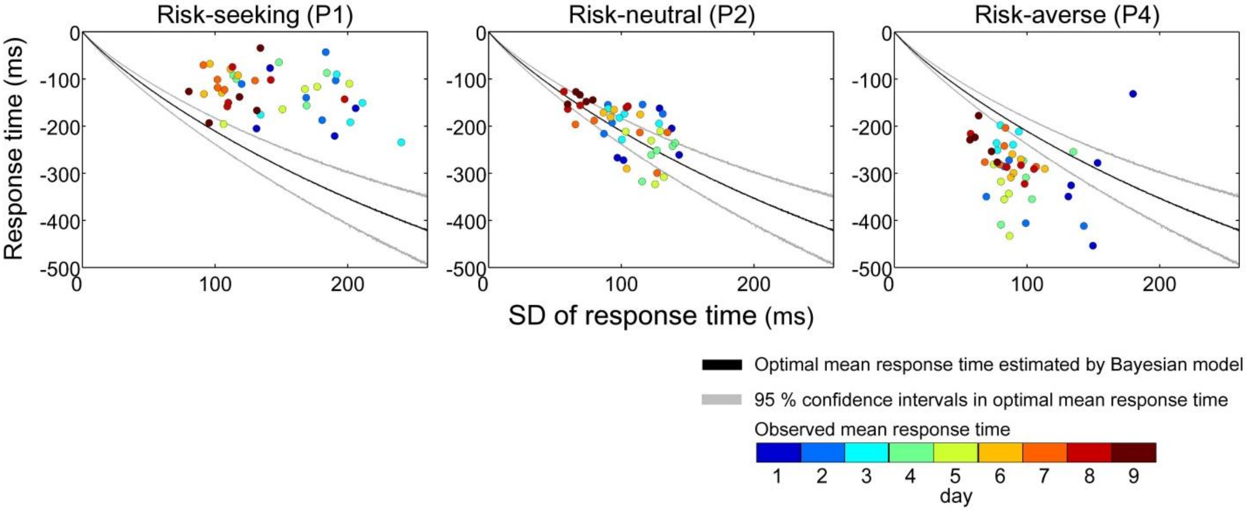


Figure 4-6. Inter-personal differences in strategy under risk.

Each panel shows a participant classified as risk-averse, risk-neutral, and risk-seeking. In each panel, the observed mean response times for all 45 blocks were plotted against the SD of the response time. The color scale of the circles indicates the day of the measurements. Black curves indicate the optimal mean response time calculated by the Bayesian model (Equation 4-2). Gray curves show the 95% confidence intervals of the optimal mean response times after 3000 bootstrap replications. For the results of the other participants, see Figure 4-7.

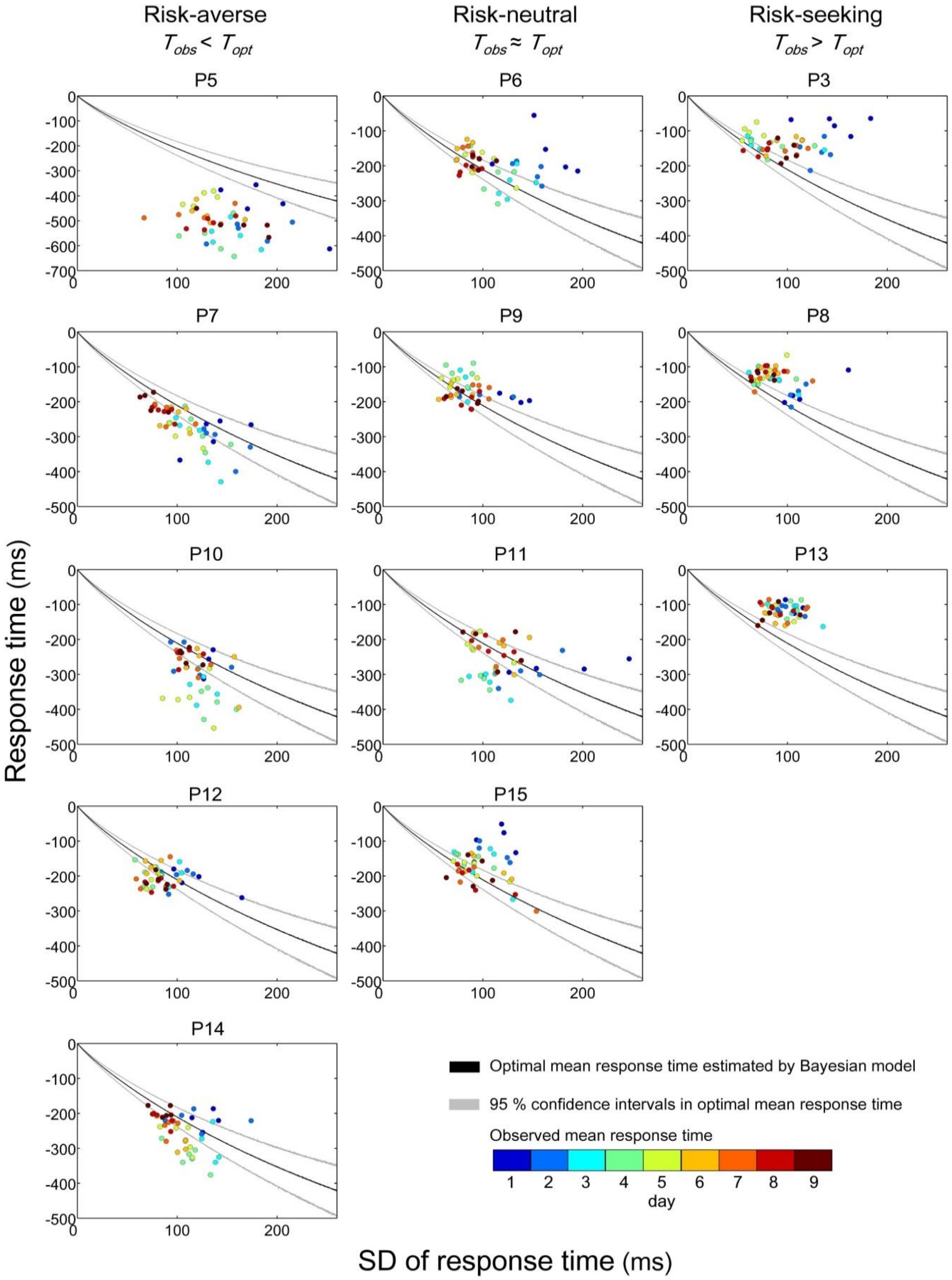


Figure 4-7. Inter-personal differences in strategy under risk.

Figure captions are similarly to Figure 4-6. In last 10 blocks (i.e., day 8 & day 9), participants in the right column are classified as risk-seeking and participants in the left column as risk-averse. Participants in the middle column are classified as risk-neutral.

4-4. Discussion

Sub-optimality in motor planning and motor control has been investigated over the last decade (Nagengast et al., 2010, 2011a, 2011b; O’Brien & Ahmed, 2013; Ota et al., 2015; Wu et al., 2006, 2009). For example, O’Brien & Ahmed (2013) used a gain function in which a higher gain was accompanied by risk of zero or negative gain. Under such an asymmetric configuration, suboptimal risk-seeking behavior was confirmed in reaching tasks and whole-body movement tasks O’Brien & Ahmed (2013). I also exploited a similar gain function for a coincident timing task and confirmed that humans tend to take higher risk than optimal under the asymmetric gain function, regardless of the location of the penalty region, as shown in Chapter 2. Chapter 3 demonstrated that this tendency was robust if the spatial motor task (i.e., a golf putting task) was applied.

A question that arose from these previous studies was related to the trainability of the motor decision. In other words, it has been unclear whether humans could update their motor planning to achieve maximum expected gain by observing the total gain of an experimental block and by repeating blocks many times. In this study, I found that ten of fifteen participants behaved sub-optimally even after 9 days or 45 blocks of practice. The SD of response time changed until day 4, while the difference between the observed mean response time and the optimal mean response time, or the distortion of the utility function changed until day 2. The participants showed consistent risk-sensitive behavior (adopting a risk-seeking or risk-averse strategy) throughout the practice. Thus, humans contradict a Bayesian decision maker who can calculate the optimal strategy for any combination of gain/loss function, as well as the probability distribution of the motor output (Hudson et al., 2012). Taken together, Chapter 4 indicate that it is relatively difficult to improve the computational ability for planning an optimal aiming point through repeated practice.

Motor learning studies have exploited motor tasks in which the position of the target at which participants should aim was clearly designated. In these situations, humans can learn a less variable motor response to a target (Kudo et al., 2000; Kudo & Ohtsuki, 2008; Lee & Carnahan, 1990; Lee et al., 1997; Shea & Kohl, 1991; Sherwood, 1988) and can also adapt movement to reach a target under a novel environment, with perturbation produced by visuo-motor rotation or force field (Hirashima & Nozaki, 2010; Ikegami et al., 2012; Lackner et al., 1994; Shadmehr & Mussa-Ivaldi, 1994; Smith et al., 2006; Takiyama & Shinya, 2016; Thoroughman & Shadmehr, 2000). The basic model of motor learning proposes that learning occurs by updating the internal model based on an error (discrepancy) between the target and the resulting motor output in a trial-by-trial basis (Ikegami et al., 2012; Smith et al., 2006; Thoroughman & Shadmehr, 2000). Humans can adapt to a novel environment and reach a particular target within 100 trials (Lackner et al., 1994; Smith et al., 2006).

In this task, a target (an aiming point) was not designated and had to be learned. Thus, an error against the explicit target was not shown to the participants in trial-by-trial manner. Instead, they were required to update their motor planning (an aiming point) based on a distribution of motor output in a block-by-block manner. The results suggested that 45 blocks (2250 trials) were not sufficient to establish such learning of an aiming point. Knowledge of the motor output distribution is accumulated by observing the result of the output in a trial-by-trial basis. In this task, therefore, the participants needed to update their aiming point (mean response time), based on the observed distribution among blocks, while compensating for the error between their implicit aiming point and their result of motor output in a trial-by-trial manner. In addition, because the optimal aiming point depends on motor variability, it can change with the reduction of variance caused by repetition of trials. For these reasons, the learning of an aiming point can be difficult and requires many trials.

Why did participants persist in adopting a suboptimal risk-seeking/risk-averse strategy? In the statistical/Bayesian decision-making model, integration of the product of gain function and motor variability determines the expected gain and optimal motor plan (Equation 4-2). If the subjective evaluation of these two functions was distorted from objective reality, the equation would yield a suboptimal motor plan. In the field of behavior economics, prospect theory (Kahneman & Tversky, 1979) and cumulative prospect theory (Tversky & Kahneman, 1992) have proposed that suboptimal economic decisions are due to a distortion of the utility from the actual gain/loss and a distortion of the probability weighting from the actual probability (Figure 1-1). Previous studies have confirmed risk-sensitive behavior in a motor task and have explained the reason from the basis of the prospect theory (Nagengast et al., 2011b; O’Brien & Ahmed, 2013; Wu et al., 2009). Based on these studies, I will discuss two possible reasons for risk-seeking/risk-averse behaviors in below.

One would be a distortion in the utility of the gain function (O’Brien & Ahmed, 2013). In the study of O’Brien & Ahmed (2013), participants over-weighted point rewards and under-weighted point penalties under a similar gain function as in the Risk condition, in which higher gain comes with the penalty (called the “cliff paradigm”). They showed that most participants adopted risk-seeking behavior and suggested that this subjective weighting of rewards/penalties could be one reason for risky planning. In contrast, risk-averse decisions could arise from a concave utility function, which indicates a decaying utility in comparison to the actual reward (Lee, 2005). In this study, I also estimated the participant’s utility function of the rewards from their actual planning data, and found that the participants showed a consistent trend in the direction of the distortion (concave or convex utility function). A further reason may be that risk-avoiders may be discouraged from responding late under Risk condition due to a penalty. In this study, the participants received a penalty involving an unpleasant alarm if they achieved zero gain. Although the volume of the alarm was the same for all participants (see Methods), the utility of the penalty may be different between them, which also possibly influenced individual motor planning.

A second possibility would be a distortion in the probability weighting of one's own motor output (Nagengast et al., 2011b; O'Brien & Ahmed, 2013; Wu et al., 2009). Despite the importance of possible motor errors of one's own upcoming action (prospective error) in motor learning (Takiyama et al., 2015), the subjective assessment of the prospective error may be unreliable. In the study of Nagengast et al. (2011b) and Wu et al. (2009), participants under-weighted small probabilities and over-weighted moderate to large probabilities when required to point to either 1 of 2 targets, in which the hit probabilities differed. Most participants exhibited risky choice behavior (Nagengast et al. 2011b; Wu et al., 2009) because these distortions led participants to believe that they had smaller movement variability than they actually had (O'Brien & Ahmed, 2013). These researchers have also shown that some participants show an opposite distortion pattern (overweighting small probabilities and underweighting moderate to large probabilities). Therefore, these studies suggest that risk-seekers in this study would underestimate their own response variance, whereas risk-avoiders would overestimate their own variance. The underestimation of motor variance was also seen in a temporal task (Mamassian, 2008) as well as in a spatial task. In this experiment, however, I could not determine which distortions (rewards/penalties or probabilities) mostly affected participant's behavior, because I could only estimate one parameter. This point should be investigated further in future.

Importantly, suboptimal behaviors were still observed on the 9th day. This indicated that an inappropriate representation of one's own variance might be retained throughout the practice. A previous study has also confirmed the evidence of an inaccurate internal model of own motor error after extensive training (Zhang et al., 2013). In the study by Zhang et al. (2013), participants assumed their own endpoint variance in the reaching task to be isotropic distribution, rather than the actual anisotropic distribution, even after hundreds of trials. In other situations, participants represented their visuo-motor error distributions as a mixture of small (2–6) sets of non-overlapping uniform distributions, rather than a single Gaussian distribution, even though their actual motor errors closely approximated a Gaussian distribution (Zhang, Daw, & Maloney, 2015). In this experiment, the participants performed the timing task for 2250 trials in total. Taken together, human probability interpretation can be distorted from the true distribution in sensorimotor output, and this inaccurate interpretation is difficult to improve solely by observing the motor outputs repeatedly.

The evidence that humans can select a movement trajectory that minimizes task-relevant movement variance (Harris & Wolpert, 1998; Hamilton & Wolpert, 2002; Todorov & Jordan, 2002) suggests that the motor system properly estimates its own motor variance. However, I observed inter-personal differences in the transition patterns of the observed mean response time. As shown in Figure 4-6, participant P1 (risk-seeking) demonstrated a response time that approached the reference time rather than the optimal time, from the beginning to the end of the practice. I also found such a tendency in participants P3, P8, and P13 (Figure 4-7). These participants may use a motor heuristic approach (Wu et al., 2006), in which the best strategy is always to aim closer to the maximum gain rather than to change the motor planning according to their own response variance. On the other hand, P4 (risk-averse) moved the mean response times closer to the reference time with a decrease in the response variance. This participant might consider his/her own variance, but the observed mean response times were located below the Bayesian-theoretical 95% confidence interval. Again, I found such a tendency in participants P7, P12, and P14 (Figure 4-7). Participant P2 (risk-neutral) almost appropriately changed the mean response time with the decrease in the response variance. It was also confirmed that these inter-personal differences were not due to levels of motivation, concentration, and sleepiness (see Supplementary Figure 4-2). Previous studies that had investigated motor planning under risk have shown no evidence that participants changed the mean endpoint of reaching or pointing movements, but these studies involved short periods of time (3 days at most) (O’Brien & Ahmed, 2013; Trommershäuser et al., 2003b, 2005; Wu et al., 2006). Thus, the current study presents novel evidence of individual differences in the transition of aiming in the presence of variability in motor output.

4-5. Supplementary information

4-5-1. Model assumption based on Weber's law

I calculated the optimal mean response time based on the model that takes Weber's law into account. Here I call response time as button press time from onset of a start signal (visual cue). In this model, the probability distribution of response time t was defined as a Gaussian distribution with mean T and standard deviation wT, which scaled linearly with a planned response time T with a constant coefficient of variation w (Jazayeri & Shadlen, 2010) as follows. Supplementary Figure 4-1A shows an example of distributions when w is 0.05.

$$P(t|T) = \frac{1}{\sqrt{2\pi(wT)^2}} exp\left[-\frac{(t-T)^2}{2(wT)^2}\right] \tag{S1}$$

The expected gain EG can be calculated by integrating the gain function under Risk condition $G(t)$ over the probability distribution $P(t|T)$.

$$EG(T) = \int_{-\infty}^{\infty} G(t) \cdot P(t|T)dt \tag{S2}$$

Supplementary Figure 4-1B shows the expected gain as a function of a planned response time when w is 0.05. I calculated the optimal mean response time T'_{opt} by maximizing the expected gain.

$$T'_{opt}(w) = \underset{T}{\operatorname{argmax}}\, EG(T) \tag{S3}$$

For $w =$ 0.05, the maximum expected gain is 89 points and the optimal mean response time is 2078 ms (Supplementary Figure 4-1B). As shown in Equation S3, the optimal mean response time in proportional variance model can be a function of Weber fraction.

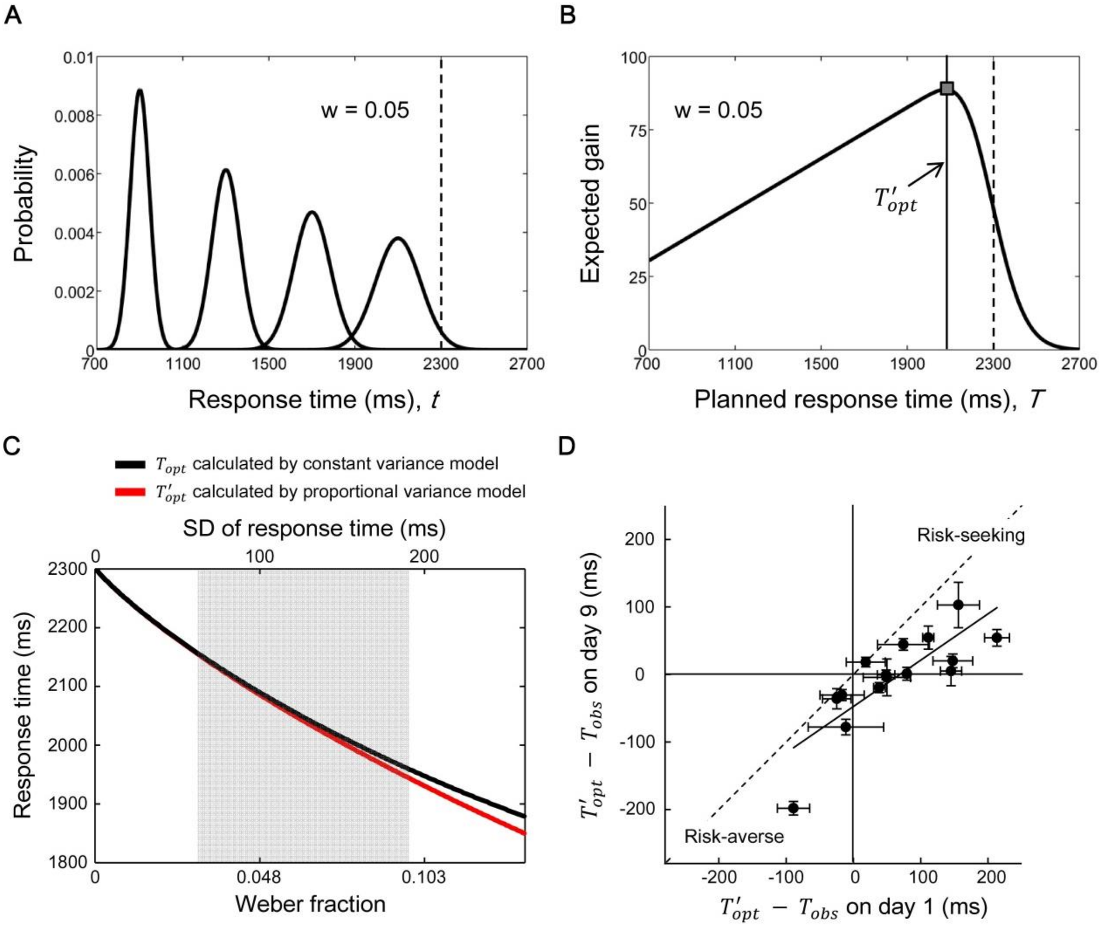
Black curves in Supplementary Figure 4-1C shows the optimal mean response time T_{opt} calculated from the model based on constant response variance (Eq. 1&2). Note that T_{opt} is a function of the SD of response time (upper horizontal axis). From the obtained relation between T_{opt} and the SD of response time, I calculate Weber fraction, $w = \frac{\sigma}{T_{opt}}$. For example, when σ

is 100 ms, T_{opt} can be 2089 ms. For these values, w can be 0.048. When σ is 200 ms, T_{opt} can be 1947 ms and w can be 0.103.

I then calculated the optimal mean response time in proportional variance model T'_{opt} from the obtained value of Weber fraction. Red curves in Supplementary Figure 4-1C shows T'_{opt} as a function of Weber fraction (lower horizontal axis). As shown in Supplementary Figure 4-1C, the deviation between T_{opt} and T'_{opt} is larger as Weber fraction or the SD of response time is larger. I show 95% confidence interval (CI) of the SD of response time obtained in the Risk condition, as the gray region. The deviation between T_{opt} and T'_{opt} was 19 ms (1951 ms - 1932 ms) in the upper limit of 95% CI ($\sigma = 190$ ms). The difference between T_{opt} and T_{obs} that I found in the experiment was clearly larger than this deviation (see Figure 4-3E).

Furthermore, based on the proportional variance model, I calculated a slope of the regression line between the difference of T_{obs} and T'_{opt} on day 1 and that on day 9. I found it to be a slope of 0.69 (Supplementary Figure 4-1D). A regression slope between the difference between T_{obs} and T_{opt} on day 1 and that on day 9 was 0.70 (Figure 4-4A).

I also conducted an additional experiment to measure participant's Weber fraction. In this experiment, three participants (P2, P5, and P6) performed the task with four different timing intervals (800 ms, 2300 ms, 3800 ms, and 5300 ms) for 50 trials each. They were instructed to press a button aiming at these intervals. I assumed that participant's response variance σ^2 is a linear function of the planned response time T, $\sigma^2 = (wT + b)^2$. From the response variance and the mean response time data, I estimated w and b. The estimated w were 0.028, 0.033, and 0.037 and b were 0.064, 0.066, and 0.032 for P2, P5 and P6 respectively. For these values of w, the deviations between T_{opt} and T'_{opt} were 1 ms (2160 ms - 2159 ms), 3 ms (2140 ms - 2137 ms), and 3 ms (2125 ms - 2122 ms).



Supplementary Figure 4-1. Model assumption based on Weber's law.

(A) The probability distribution of response time with Weber fraction w. The temporal variance is proportional to a planned response time. Here I show an example of distributions when w is 0.05. (B) Expected gain as a function of a planned response time for $w = 0.05$. The vertical line indicates the optimal mean response time. (C) Comparison of 2 models. Black curves represent the optimal mean response time based on constant variance model T_{opt}. This is calculated as a function of the SD of response time (upper horizontal axis). Red curves represent the optimal mean response time based on proportional variance model T'_{opt}. This is calculated as a function of Weber fraction (lower horizontal axis). Gray region indicates 95% confidence interval (CI) of the SD of response time obtained in the Risk condition. From the additional experiment, we obtained three participant's Weber fraction ($w =$ 0.028, 0.033, and 0.037). For these values of w, there are marginal deviations between T_{opt} and T'_{opt}. (D) Linear regression analysis. A slope of the regression line between T_{obs} and T'_{opt} on day 1 and that on day 9 resulted in 0.69.

4-5-2. Consistency of motor planning under risk

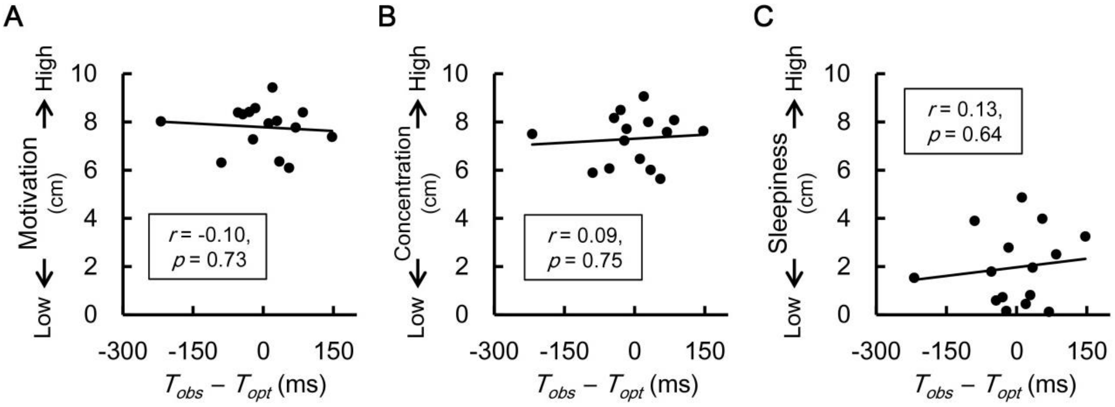
I performed a regression analysis between the differences of T_{obs} and T_{opt} from day 1 to day 9. Supplementary Table 1 shows the regression matrix. A slope of a regression line, 95% confidence intervals (CI) of slope, a coefficient of determination (R^2), and P value are plotted.

Supplementary Table 4-1. Regression matrix of the difference of T_{obs} and T_{opt}

			$T_{obs} - T_{opt}$ on							
			D2	D3	D4	D5	D6	D7	D8	D9
$T_{obs} - T_{opt}$ on	D1	Slope	1.06	0.97	1.10	0.85	0.80	0.83	0.71	0.70
		95% CI of slope	0.68-1.45	0.52-1.43	0.61-1.59	0.49-1.21	0.48-1.12	0.46-1.20	0.25-1.17	0.41-0.998
		R^2	0.73	0.62	0.65	0.67	0.69	0.64	0.46	0.67
		P value	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
	D2	Slope		0.88	0.99	0.76	0.70	0.75	0.74	0.65
		95% CI of slope		0.61-1.15	0.69-1.28	0.56-0.97	0.52-0.89	0.53-0.96	0.51-0.97	0.52-0.78
		R^2		0.79	0.80	0.83	0.83	0.81	0.79	0.90
		P value		0.00	0.00	0.00	0.00	0.00	0.00	0.00
	D3	Slope			1.08	0.72	0.68	0.78	0.75	0.64
		95% CI of slope			0.94-1.23	0.47-0.98	0.46-0.91	0.60-0.96	0.52-0.98	0.47-0.80
		R^2			0.95	0.74	0.77	0.88	0.79	0.84
		P value			0.00	0.00	0.00	0.00	0.00	0.00
	D4	Slope				0.68	0.62	0.71	0.67	0.58
		95% CI of slope				0.48-0.88	0.42-0.82	0.57-0.86	0.46-0.89	0.44-0.72
		R^2				0.80	0.78	0.89	0.78	0.85
		P value				0.00	0.00	0.00	0.00	0.00
	D5	Slope					0.82	0.88	0.87	0.74
		95% CI of slope					0.57-1.08	0.60-1.15	0.57-1.17	0.52-0.96
		R^2					0.79	0.78	0.75	0.80
		P value					0.00	0.00	0.00	0.00
	D6	Slope						0.98	1.01	0.85
		95% CI of slope						0.73-1.24	0.77-1.25	0.68-1.02
		R^2						0.84	0.87	0.90
		P value						0.00	0.00	0.00
	D7	Slope							0.96	0.81
		95% CI of slope							0.76-1.16	0.68-0.93
		R^2							0.89	0.94
		P value							0.00	0.00
	D8	Slope								0.79
		95% CI of slope								0.65-0.93
		R^2								0.92
		P value								0.00

4-5-3. Visual analog scale

To establish whether participant's motivation, concentration, and sleepiness influenced risk-sensitivity, I conducted a correlation analysis. The levels of 3 scales were evaluated by VAS. The correlation analysis showed that there was no significant relationship between the average difference of the observed mean response time T_{obs} and the optimal mean response time T_{opt} in all 45 blocks and the average motivation (r = - 0.10, p = 0.73, df = 15), concentration (r = 0.09, p = 0.75, df = 15), and sleepiness (r = 0.13, p = 0.64, df = 15). Therefore, inter-personal differences in strategy under risk were not due to the differences in motivation, concentration, and sleepiness.



Supplementary Figure 4-2. Visual analog scale.
No correlation between the motor planning under risk and the levels of motivation (A), concentration (B), and sleepiness (C). Each symbol represents each participant.

Chapter 7.

General discussion

7-1. Summary of the results

The present thesis aimed to elucidate characteristics of decision-making in the motor tasks with an asymmetric gain function. In order to investigate it in detail, five separate studies were prepared in the present thesis. First of all, the main findings in each study are summarized.

Throughout the thesis, I modeled an ideal motor decision-making of an aiming point based on Bayesian decision theory (BDT; Blackwell & Girshick, 1954). BDT is a powerful mathematical model for selecting an optimal action under uncertainty (Berger, 1980; Maloney & Zhang, 2010). For given participant's sensory motor uncertainty, I defined their optimal aiming point for maximizing the expected gain and then compared it with participant's actual aiming point. Based on the relation between the ideal and the observed aiming point, I divided participant's strategy into three types: risk-neutral in which the actual aiming point agrees with the optimal point, risk-seeking in which it locates closer to risk of zero gain than the optimal point, and risk-averse in which it locates further from risk of zero gain than the optimal point.

In Chapter 2, the relationship between the optimality of motor plan and the configuration of the gain function was addressed. To this end, I tested two configurations of the gain function. It was revealed that the actual temporal planning was well agreed with the ideal planning under symmetric configurations of gain function, whereas a discrepancy was found under asymmetric configurations of gain function in which higher gain was accompanied with penalty (Table 2-1). Participants took risk-seeking strategy and this behavior held when the location of the penalty region was altered (Figure 2-5). Moreover, overcompensation for own temporal error following miss trial was found from trial by trial analysis (Figure 2-6). These results proposed that temporal planning can be suboptimal when the gain function is asymmetric.

Chapter 3 examined whether such risk-sensitive decision is specific tendency for a coincident timing task or not. The result demonstrated that it was also confirmed in a golf putting task in which spatial action plan is required and implicit changes in motor output variability induced by signal-dependent-noise does not alter participant’s planning largely under the asymmetric gain function (Figure 3-4 & Figure 3-5B). Therefore, Chapter 3 concludes that the configuration of the gain function leads decision making to be risk-sensitive regardless of a type of motor tasks.

However, there is the possibility that a repetitive practice improves decision-making to be risk-neutral and humans can learn to aim optimally by observing the results of their own motor output repeatedly. Thus the effect of leaning on suboptimal motor planning was investigated in Chapter 4. Chapter 4 exploited a coincident timing task and conducted a learning experiment that lasted 9 days. Similar to previous findings of motor learning studies, temporal variance gradually decreased by practicing the task (Figure 4-3D) and this resulted in increasing the expected gain that participants obtained (Figure 4-3A). However, the effect of learning on temporal aiming point was not always confirmed for all participants (Figure 4-3E). Generally, participants persisted in adopting the strategy that they preferred on the first day of the practice, throughout the practice (Figure 4-4A). Inter personal difference that how risk-seeking or risk-averse individuals update their aiming point was also confirmed. Risk-seeking individuals demonstrated mean response times that approached the reference time (maximum one-trial gain) than optimal times from the beginning to the end of the practice (Figure 4-6 & Figure 4-7). In contrast, risk-averse individuals gradually moved the mean response times closer to the reference time with a decrement in the response variance, but it located below than the optimal times (Figure 4-6 & Figure 4-7). These results provide us strong evidence that it is difficult to learn the optimal aiming point solely by observing the results of own motor output repeatedly. In other words, these results suggest that constraint in decision-making can be a factor for hindering the progress of motor skill learning.

In Bayesian decision theory, integration of the product of gain function and motor output distribution determines the expected gain and optimal motor plan. If the subjective representation of own motor distribution distorted from objective reality, the model would yield a suboptimal motor plan. Therefore, Chapter 5 examined the possibility that the limitation in our memory capacity, for building on an accurate representation of own motor distribution from the repeatedly observed motor output error, results in a suboptimal motor plan. In the experiment, the endpoints of reaching movement in all trials were informed to participants after the end of each practice task (Figure 5-3B), which intended to build on an accurate representation of endpoint distribution. The participants continued to practice the task receiving this distribution feedback. Although three of eleven participants switched their motor plan by the feedback, the rest of the participants retained risk-seeking or risk-averse strategy (Figure 5-7B), similar to the result in Chapter 4. Overall, there was no difference between feedback group and no feedback group in the difference between the observed and the optimal motor plans, as well as in the observed gain per trial and variability of reaching movement (Figure 5-6). These results suggest that an inaccurate estimation of motor distribution is not likely to result in a suboptimal motor plan. In the additional experiment in Chapter 5, I required participants to indicate their subjective optimal aiming point to maximize the expected gain in Gaussian distribution and unimodal uniform distribution (Supplementary Figure 5-2A). In Gaussian distribution, the probability of earning higher gain increases as they allow risk of zero gain by aiming closer to the maximum gain, while it decreases as they do not allow risk of zero gain by aiming further from the maximum gain. On the other hand, in unimodal uniform distribution, the probability of earning higher gain is constant no matter how they allow risk of zero gain. As a result of the additional experiment, the deviation between the subjective optimal aiming point and the theoretically calculated optimal aiming point was observed in Gaussian distribution, whereas it was not observed in unimodal uniform distribution (Supplementary Figure 5-2). Based on these findings, it is likely that humans have computational limitation to find the optimal motor plan considering the trade-off between the probability of higher gain and the risk of zero gain, as a reason why it is difficult to learn to aim optimally under risk.

Finally, in Chapter 6, a neurostimulation study for revealing the role of dorsolateral prefrontal cortex (DLPFC) on risk-sensitive motor decision-making was conducted with transcranial direct current stimulation (tDCS). In previous neuroeconomics studies, it is suggested that DLPFC is involved in the suppressive control of seductive options in economic tasks (Fecteau, Knoch et al., 2007). In order to examine the causal role of DLPFC in motor decision, three different DC stimulation (right anodal/left cathodal, right cathodal/left anodal, and sham stimulation) was prepared (Figure 6-1D). The main finding is that anodal stimulation over right DLPFC coupled with cathodal stimulation over left DLPFC induced to move mean response time further from the reference time (i.e., one-trial maximum gain) and thus reduced a risky motor plan (Figure 6-2&Figure 6-3). Right cathodal stimulation with left anodal stimulation over DLPFC or sham stimulation did not affect a motor plan (Figure 6-2&Figure 6-3). Furthermore, it is shown that these three stimulations did not influence temporal variance and mean response time in the task involving no risks (Figure 6-5), which suggest that disruption of the temporal processes is not likely to alter mean response time. These results proposed the possibility that dorsolateral prefrontal cortex contributes to risk-sensitive decision-making in the motor task.

7-2. Integration of the results obtained from the present study with previous decision-making studies

As reviewed in Introduction, Trommershäuser et al. (2003a; 2003b; 2005; 2008) claimed that human behavior in motor tasks comes close to the model of Bayesian decision theory and thus motor decision-making is risk-neutral. However, series of these studies have used the motor task in which participants obtain either high gain, moderate gain, negative gain, or zero gain (Figure 1-4A). Therefore, a constant value of gain is on the edge of risk of zero gain. In contrast to this gain structure, the present thesis investigated motor decision-making under the gain function in which higher values of gain come with risk of zero gain, considering a feature of gain structure in sports. The present thesis showed it to be risk-sensitive.

Wu et al. (2006) suggested that deviation from optimality arises if the complexity of a motor plan increases. These researchers showed that the optimal plan could be adopted when the optimal endpoint lies within the target circle which gave positive gain, which is the same task as the one used in Trommershäuser et al (2003a; 2003b; 2005; 2008), whereas the suboptimal plan could be adopted when it lies within the penalty circle (i.e, it is more difficult to aim within the penalty circle than to aim within the target circle). Furthermore, even in the same gain structure as the one used in Trommershäuser et al (2003a; 2003b; 2005; 2008), it is shown that performance dropped below optimal when the penalty circle was displayed 400 ms after movement onset and late responses (>700 ms) were heavily penalized (Trommershäuser, Mattis, Maloney, & Landy, 2006). In the asymmetric gain function used in this thesis, the optimal aiming point is not predetermined since it depends on the standard deviation of participant’s motor output distribution (i.e., Gaussian distribution). From these findings, it is assumed that the more difficulty a motor plan is, the larger deviation from the optimal plan occurs. However, it is not unclear where a boundary line to determine the optimality or the sub-optimality is. It is assumed that the gain function used in this thesis is just one of a case in sub-optimality.

Therefore, a theoretical framework to determine the optimality or the sub-optimality in a unified manner should be built on in the future study.

The results found in the present thesis are consistent with previous economic and psychological studies claiming irrationality of decision making. Kahneman & Tversky accounted for risk-sensitive decision process with value function and probability weighting function (Kahneman & Tversky, 1984; Tversky & Kahneman, 1992). Value function captures human’s subjective value of outcome relative to a reference point with a concave shape for gains and a convex shape for losses (Figure 1-1A). Probability weighting function captures human’s subjective distortion of probability and suggests that human over-weights small probabilities and under-weights mid-to-high probabilities (Figure 1-1B). Such distortions in objective outcome and objective probability lead inconsistent choice behavior (preference reversal) and loss aversion (Kahneman & Tversky, 1984). Based on these findings, I also explained participant’s suboptimal behavior by introducing value (i.e., utility) function in Chapter 4. As a result of fitting the data, the participant’s behavior could be approximated by non-linear (concave or convex) utility function (Figure 4-5).

Chapter 5&6 examined whether feedback information of motor output distribution or neurostimulation can improve a suboptimal motor plan. Chapter 5 gave participants an accurate knowledge about own motor distribution which helps them to maximize the expected gain. However, eight of eleven participants retained their motor plan that they preferred before feedback period. This result indicates that it is difficult to find an objective optimal aiming point for participants even if they know their own motor distribution accurately. Nevertheless, Chapter 6 demonstrated that bilateral transcranial direct current stimulation (tDCS) over DLPFC reduced a risky motor plan. It is suggested that anodal stimulation over right DLPFC with cathodal stimulation over left DLPFC leads to pump a balloon less often in a risk task in which higher rewards could be obtained by pumping it more often (Fecteau, Pascual-Leone, et al., 2007). This polarity (electrode position) also leads to choose safer lottery more often (Fecteau, Knoch, et al., 2007) and reduces craving level of alcohol (Boggio et al., 2008) and cigarettes (Fecteau et al., 2014). Furthermore, in Chapter 5, I confirmed that participants who showed large score for gladness to higher one-trail gain more likely took risk-seeking strategy (Supplementary Figure 5-1A). Considering these findings, it is likely that right anodal with left cathodal tDCS of DLPFC leads participants to avoid aiming closer to maximum gain by activating a function for suppressing sensitivity to take higher one-trial gain. In addition, it is suggested that decision-making is influenced by emotion and feeling (Bechara, 2004). Therefore, considering the results obtained in this thesis and the results found in previous studies, the present thesis proposes that the decision-making system in motor tasks consists of not only a dry system that follows Bayesian decision theory and executes optimal computing, but also a wet system that is influenced by sensitivity to rewards and risks.

7-3. Integration of the results obtained from the present study with previous motor control and motor learning studies

It has been widely examined how we learn new motor skill and how we control our movement. To understand these mechanisms, previous motor learning and motor control studies have exclusively exploited motor tasks in which the position of the target at which participants should aim was clearly designated. In such situation, humans can adapt movement to reach a target even when an externally produced perturbation disturbs their movement (Lackner et al., 1994; Shadmehr & Mussa-Ivaldi, 1994; Thoroughman & Shadmehr, 2000) and thus humans can learn a less variable motor response to a target (Kudo et al., 2000; Lee & Carnahan, 1990; Shea & Kohl, 1991; Sherwood, 1988). The basic model of motor learning describes such learning process by state-space model which proposes that learning occurs by updating the internal model based on an error (discrepancy) between the target and the resulting motor output in a trial-by-trial manner (Ikegami et al., 2012; Smith et al., 2006; Thoroughman & Shadmehr, 2000).

In motor control studies, it has been investigated how humans achieve movement trajectory to reach a target. Although there are many possible movement paths with various velocities from an initial position to the target, humans pick up the nearly straight path with a bell shaped velocity profile. Early studies to modeling this movement trajectory have suggested that humans select “single deterministic trajectory” that optimizes the trade-off between the goal of the movement and the biomechanical cost. Possible biomechanical cost functions, suggested in the previous studies, include jerk change (Flash & Hogan, 1985), torque change (Uno et al., 1989), and muscle tension change (Dornay et al., 1996). Late studies have suggested that humans select the movement trajectory that minimizes positional variance at the end of the movement, taking biological noise in motor system into account (Harris & Wolpert, 1998; Hamilton & Wolpert, 2002). Both models have successfully accounted for the nearly straight trajectory with a bell shaped velocity profile. These studies indicate that the motor system achieve the movement trajectory to reach the target by solving the optimization problem in which cost function to be minimized is biomechanical cost or movement variability.

If the light in an experimental room is bright, the position of the target is easy to be detected. If it is unclear due to the darkness of the light, how humans detect the position of the target? Bayesian integration allows us to select the optimal action plan based on the posterior probability distribution in face of sensory, motor, and task uncertainty (Körding & Wolpert, 2006; Wolpert & Landy, 2012). In this situation, prior knowledge about the target location, as well as current sensory information about unclear target location is needed to estimate the target location. By integrating these two information, the posterior information about the target location can be obtained and thus likelihood action plan for hitting the target can be selected. It has been shown that the model of Bayesian integration has successfully predicted actual human behavior for detecting unclear target position (Acerbi et al., 2014; Berniker et al., 2010; Tassinari et al., 2006; Vilares et al., 2012). Bayesian integration has also been shown to occur during sensory motor learning (Körding & Wolpert, 2004), timing estimation (Jazayeri & Shadlen, 2010; Miyazaki et al., 2005), and temporal order judgment (Miyazaki et al., 2006) to achieve the optimal estimation of relevant stimulus.

Taken together, these studies suggest that if the position of the target to reach out the target is designated, humans can achieve the optimal movement trajectory minimizing the biomechanical cost or the variance of movement endpoint and can update the motor command based on the observed error. Furthermore, humans can select the likelihood action plan for reaching out the target under sensorimotor or task uncertainty. However, in the task used in this thesis, the target was not designated. The participants had to decide where they should aim and learn the optimal aiming point based on a distribution of motor output. The present thesis showed that the learning of aiming point is not easy to be established. For the reason of this difficulty, the present thesis suggested that it is related to the limitation of computational facilities for integrating the asymmetric gain function over motor variability, rather than the limitation of memory capacities for building an accurate representation of motor variability. Therefore, considering the results found in this thesis and the previous studies, the present thesis proposed that there is the difference between the computational ability for controlling a movement or learning a motor command to reach out the designated target and the computational ability for deciding the optimal target in our motor system.

7-4. Brain regions related to components of Bayesian decision theory

Recent studies have revealed brain regions related to components of statistical/Bayesian decision theory (i.e., gain function and motor uncertainty). For example, it has been suggested that broad regions, including the ventromedial prefrontal cortex (vMPFC)/the oribitofrontal cortex (OFC), the ventral striatum, and the insula, are involved in value representation in the human brain (for review, see Bartra et al., 2013; Levy & Glimcher, 2012; Peters & Büchel, 2010). Particularly, Levy & Glimcher (2012) and Peters & Büchel (2010) showed that the vmPFC/OFC is the overlapping region that represents subjective value across different types of rewards, by conducting a meta-analysis. These findings suggest that vmPFC/OFC reflects the distortion of the utility from the actual rewards.

The dorsal premotor cortex (PMd) and the primary motor cortex (M1) have been reported to contribute to motor uncertainty. It has been demonstrated that, in nonhuman primates, movement variability arises from variation in neural activity in PMd and M1 (Chaisanguanthum et al., 2014; Churchland et al., 2006). How does the brain represent such motor uncertainty? Wu et al. (2011) showed that the probability weight is represented in the medial prefrontal cortex (mPFC) when probability information is implicit in the participant’s own motor noise and needs to be estimated. In the task used in this thesis, an accurate estimation of motor uncertainty was needed to calculate the Bayesian optimal solution. For instance, confounding the 4% miss trials (i.e., responding after the reference time) with 3% resulted in a difference of 57 ms in the risk-neutral response time (calculated by simulation, data not shown). The brain may need much time to estimate the prospective error with such accuracy.

By integrating the gain function and motor uncertainty, the expected gain and optimal motor plan were determined in the statistical/Bayesian decision-making model. Little is known about the neural representation involved in the integration of these 2 sets of information. Ting et al. (2015) investigated the neural mechanisms underlying Bayesian integration using a decision-making task in which participants were required to estimate the reward probability by combining past experience (prior knowledge) with current sensory information (likelihood), and showed that the mPFC plays a role in this Bayesian integration. In future studies, it would be interesting to investigate how the brain integrates a gain function over inherent motor uncertainty and how the brain makes a motor decision.

7-5. Significance of the present thesis

Again, the present thesis aimed to elucidate the characteristics of decision-making in motor tasks under an asymmetric gain function in which higher gain comes with risk of zero gain. This gain structure can be seen in various sports, such as tennis, table tennis, football, baseball, golf, alpine ski, ski jump, and so on[1]. For example, in tennis, a ball bouncing as close as possible to the line marking the edge of the court would result in scoring a point, while a ball bouncing beyond the line would cost the player a point. In such a situation, the position of the target at which players should aim is not overtly designated, and thus players should decide where they aim for by themselves.

A number of sports science studies have investigated the characteristics of muscle activation and the biomechanical properties to achieve the movement that was determined by experimenters (for example, throwing a ball toward a target quickly or kicking a ball toward the target powerfully) and have demonstrated the differences between skilled players and novice players (for example, Fujii et al., 2009; Fleisig et al., 1999). These studies have provided useful practical implications to coaches and trainers in various sports fields. However, it should be noted that the improvement of sports performance cannot be fundamentally achieved without an appropriate decision-making. The present thesis focused on the characteristic of motor decision-making and found that it is difficult to learn an optimal decision even through repetitive practice. Therefore, the present thesis revealed that constraint in decision-making can be a factor for hindering the progress of motor skill learning by introducing a novel view that the previous sports science studies have missed.

1: There are several sports that have a symmetric gain structure, such as archery and shooting. In these sports, a gain is distributed symmetrically around the center of the target. Therefore, accuracy in hitting the center of the target is a crucial factor for performance.

7-6. Practical implication for coaching methods in sports field

Considering the findings that are stated above, it is expected that their performance can be maximized by altering the strategy. Figure 7-1A shows the expected gain that the participants actually earned in 9 day’s learning experiment. The expected gain was improved from day 1 to day 4 (this effect is visualized as a blue region) due to the decrease of response variance but it reached a plateau thereafter. It also deviated from the expected gain that the participants theoretically earned (this difference is visualized as a red region). Therefore, their performance would be improving by reducing this difference.

For coaching methods in the sports field, it is important to provide an appropriate guidance considering an individual difference in risk-handling strategy. Left panel in Figure 7-1B shows risk-averse individual. This participant moved the mean response times closer to the reference time (this effect is shown as a blue region) as practice progressed, but his scope of the search was limited to avoid a miss-trial, as shown in a blue region. Thus for risk-avoiders, it would be important to teach them to expand it as shown in a red region and make them experience a miss-trial. In tennis, the proper instruction would be to aim to hit an ace more aggressively, rather than to aim safely within the court. In contrast, risk-seeking individual consistently aimed closer to the reference time than the optimal response time (Figure 7-1B right panel). In the long run, for risk-seekers, it would be important to wait until their response variance has decreased (this effect is shown as a red region), rather than to teach them to avoid risk. In tennis, this would mean to wait for the development of the skill level, even though the individual frequently loses a point by aiming for an ace when the skill level is still poor.

In fact, risk-seeking behaviors are seen in extensively trained players (Neiman & Loewenstein, 2011; Skinner, 2012). For example, professional NBA basketball players tend to attempt a consecutive 3-point shot after making a successful 3-point shot more often than after failing to do so, even though the chance of making a further 3-point shot successfully and the average number of points gained by an offensive team is decreased (Neiman & Loewenstein, 2011). NBA players are also unwilling to shoot during an early stage of the shot clock even though higher points per possession can be obtained by shooting more frequently, possibly due to overconfidence about shot opportunities during later stages (Skiner, 2012). Therefore, coaching methods to evaluate each player’s strategy under risk, as well as their skill level, would contribute to achieving superior performance in beginners as well as of experts in a variety of sports.

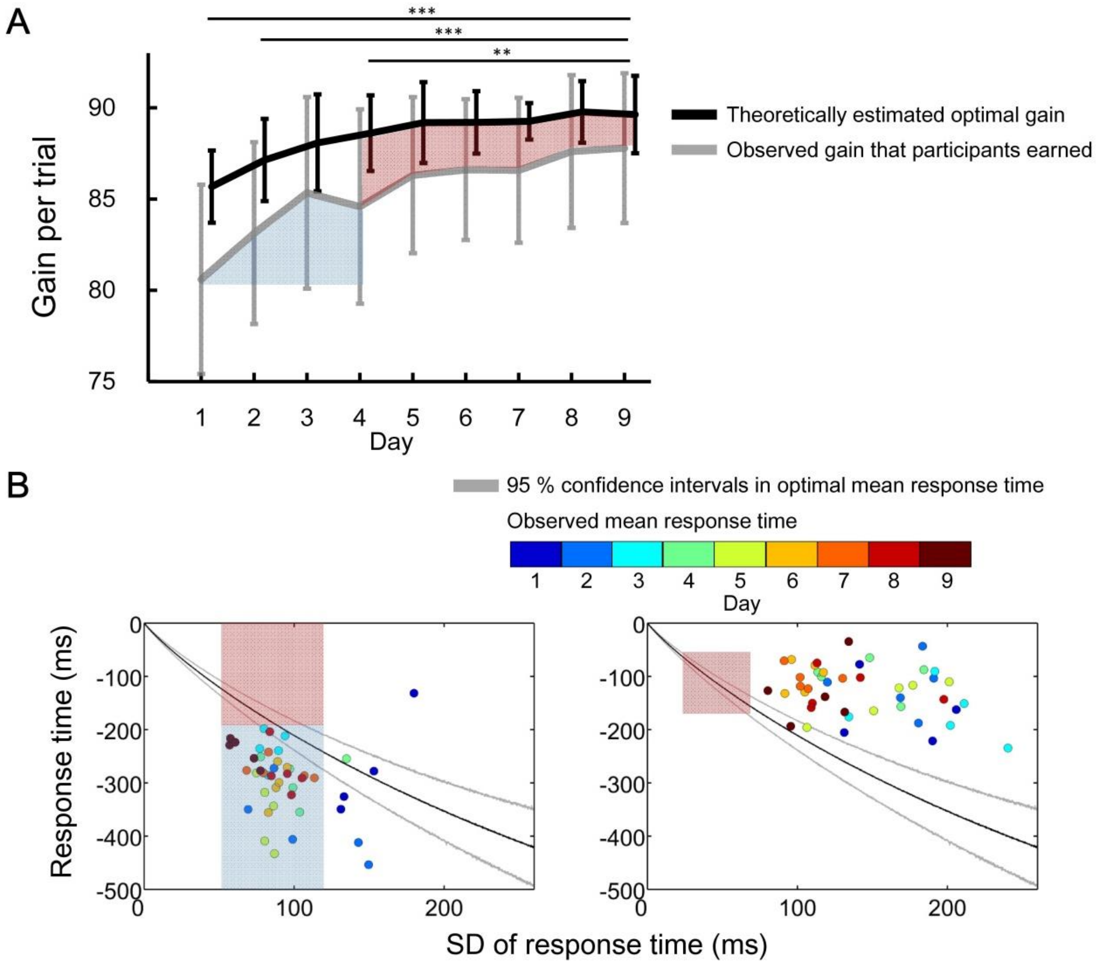


Figure 7-1. Practical implication for coaching methods.

(A) Risk-sensitive strategy results in the difference between the optimal and observed gain. *** indicates $p < 0.001$ and * indicates $p < 0.05$ compared with day 9. (B) Typical two participants who persisted risk-averse (left panel) and risk-seeking strategy (right panel).

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