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THE EFFECTS OF REWARD AND RISK LEVEL ASSOCIATED WITH SPEEDED
ACTIONS:
EVIDENCE FROM BEHAVIOR AND ELECTROENCEPHALOGRAPHY

A Thesis Presented
by
XINGJIE CHEN

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
Of the requirements for the degree of

MASTER OF SCIENCE

September 2018

Psychology

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XINGJIE CHEN

Approved as to style and content by:

Youngbin Kwak, Chair

Joonkoo Park, Member

David Moorman, Member

Caren M. Rotello, Department Head
Department of Psychological and Brain Science

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ABSTRACT

THE EFFECTS OF REWARD AND RISK LEVEL ASSOCIATED WITH SPEEDED ACTIONS: EVIDENCE FROM BEHAVIOR AND ELECTROENCEPHALOGRAPHY

SEPTEMBER 2018

XINGJIE CHEN, B.S., CENTRAL CHINA NORMAL UNIVERSITY

M.S., UNIVERSITY OF MASSACHUSETTS AMHERST

Directed by: Professor Youngbin Kwak

Choosing a course of action in our daily lives requires an accurate assessment of the associated risks as well as the potential rewards. The present two studies investigated the mechanism of how reward and risk level influence the motor decisions of speeded actions (Chapter 2) and its neural dynamics (Chapter 3) by focusing on the beta band (15-30 Hz) oscillation patterns reflected in the EEG signals. Participants performed a modified version of the Go-NoGo task, in which they earned reward points based on the speed and accuracy of response. On each trial, the reward points at stake (120 vs. 6) and the probability that a Go signal would follow (Go-probability) were presented prior to a Go/NoGo signal (*Trial Information Period*). The behavioral results (from both Chapters 2 and 3) showed that larger amount of rewards can motivate people to respond faster, and this effect was modulated by the assessed risk, suggesting that decisions for actions are based on a systematic trade-off between rewards and risks. The EEG data showed that motor beta oscillations from the two studied brain regions reflected different levels of motivation towards a motor response across different reward and risk levels. Specifically, the lower beta power associated with higher reward and lower risk level. Collectively, the results provide a mechanistic understanding of how motivational cues are translated into action outcomes via modulating patterns of brain oscillations.

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CHAPTER 1

LITERATURE REVIEW

1.1 Introduction

Imagine yourself facing a yellow light. You can choose to press down on the gas pedal to make it through or to slow down and come to a stop. Choosing a course of action in a daily life situation as described requires an accurate assessment of the associated risks as well as the potential rewards. These assessments would entail weighing the costs and benefits of one action (e.g. speeding up to make the light) vs. the other (e.g. slowing down to come to a stop). Recent studies have shown that one relies on a systematic trade-off between the benefits and the costs as well as risks associated with an action when making these decisions, equivalent to the predictions of economic choice theory (Burke, Brunger, Kahnt, Park, & Tobler, 2013; Klein-Flügge, Kennerley, Friston, & Bestmann, 2016; Skvortsova, Palminteri, & Pessiglione, 2014). Specifically, these studies demonstrate that individuals put greater motor efforts when the potential rewards are higher and the associated risks are lower, which parallels the normative trade-offs between decision variables such as value and risk during economic decision making. These works are also in line with the important theoretical efforts in the field of visual motor control aimed at understanding movement planning and control within the framework of economic decision making (Trommershäuser, Maloney, & Landy, 2008; Wolpert & Landy, 2012). In these theoretical efforts, motor control is viewed as a problem of maximizing the utility of movement outcomes in the face of sensory, motor and task uncertainty (Wolpert & Landy, 2012), which is equivalent to economic choice scenarios under uncertainty (Platt & Huettel, 2008).

In the present thesis, I investigated the neural bases of decisions for actions. Within this

effort, I first developed a novel task paradigm to investigate how rewards and risk level influence motor decisions in speeded actions (Chapter 2). Then I investigated how the human brain evaluates reward and risk level associated with an action by focusing on the neural oscillation patterns reflected in the EEG signals (Chapter 3). In particular, I studied whether the beta-frequency oscillations involved in motor processing were modulated by the reward and risk level associated with a speeded action.

1.2 Motor Control and Decision Making

Decision making for actions is most often present in choosing to exert motor efforts towards a goal. A typical example is shown in animal foraging behavior; the animal puts forth moving around from location to location to retrieve food rewards. In doing so, they explore their environment to minimize foraging costs and maximize retrieval of foods (Bautista, Tinbergen, & Kacelnik, 2001; Kacelnik, 1997; MacArthur & Pianka, 1966).

In laboratory studies, decisions to put forth physical efforts has often been studied in relation to intrinsic motivation and external incentive rewards (Ballanger et al., 2006; D. D. Chen & Chen, 2013; Joshua & Lisberger, 2012; Mir et al., 2011; Ramnani & Miall, 2003). These studies demonstrate that presenting potential reward outcomes can lead to faster responses and exertion of greater forces during an action required for retrieving the reward. More recent work has shown that there is a systematic trade-off between physical effort and the associated rewards in humans. Specifically these studies showed that people decided to put greater physical efforts only when it would result in larger rewards (Burke et al., 2013; Hartmann, Hager, Tobler, & Kaiser, 2013; Klein-Flügge et al., 2016; Klein-Flügge, Kennerley, Saraiva, Penny, & Bestmann,

2015; Treadway et al., 2012; Wardle, Treadway, Mayo, Zald, & de Wit, 2011). This suggests that similar to the temporal delay to reward arrival, physical efforts can discount the reward value at stake.

It is important to note that risk, as well as reward, is one of the key variables of decision making under uncertainty. In general terms, risk is known as a chance of negative outcome (Mishra, 2014), such as harm, loss, and danger (Bornovalova et al., 2009; Leigh, 1999). Risk is also an important variable to consider in decisions for course of actions. For example, while one may choose to drive fast to avoid being late for work, one should also consider that speed driving increases the risk of traffic accidents. Despite its relevance to real life, not many studies have focused on how risk plays a role in decisions for actions. In one study, a statistical decision theory was developed to explain the processes underlying a motor action under risk, using a simple target-hitting task (Trommershäuser, Gepshtein, Maloney, Landy, & Banks, 2005; Trommershäuser, Maloney, & Landy, 2003a, 2003b). In this task, participants were asked to rapidly hit a target area using their fingertips in order to gain a reward and received a penalty if they hit the non-target areas. Thus the risk related with their action is proportional to their motor variability. The experimental data and the model suggested that decisions on an action was made based on one's estimate of the sensorimotor variability, which allowed controlling for their motor responses to minimize the risk associated with the movement and maximize the reward (Trommershäuser et al., 2003a). This study, however, was not designed to look at the motivational aspect of the risk-taking movements. First of all, the levels of obtainable rewards did not vary, while the magnitude of expected rewards could motivate people toward a high risk action (Doya, 2008). Furthermore, the level of risk associated with an action was not explicitly described such that one can make prior judgment on the course of action. Instead, it was

implicitly defined as a result of motor variability. Further studies considering both reward and risk in the same context is required to clarify the processes underlying decision making for an action.

One goal of the present studies is to develop a motor decision paradigm combining both reward and risk level and investigate how people evaluate the reward and risk level to make a motor decision. While “speed” is an important variable determining the characteristics of a movement, most studies have only focused on physical force in the studies of decision making for actions (e.g., Kurniawan et al., 2010; Meyniel & Pessiglione, 2014; Skvortsova et al., 2014). Movement speed is one of the most important factors influencing sensorimotor variability that is associated with risks during a movement (Trommershäuser et al., 2005; Trommershäuser et al., 2003b). Importantly, speed is naturally associated with greater risk for failure in any task performance as demonstrated in speed-accuracy trade-off (Franks, Dornhaus, Fitzsimmons, & Stevens, 2003; Pachella, 1973; Ratcliff & Tuerlinckx, 2002). Thus movement speed is one measure to look at the effects of risk in decision making for action.

1.3 Beta Oscillation in Cortico-Basal Ganglia Circuitry – Target neural mechanism

In addition to the behavioral study about the effect of reward on risk level on motor actions, I would like to further investigate the underlying neural bases of this process. Until now, the literature about motor actions focused on the cortico-basal ganglia circuitry of motor initiation and inhibition, specifically, including direct and indirect pathways as well as the hyper-direct pathway. The details of the cortico-basal ganglia circuitries were described in the following sections.

1.3.1 Direct Pathway and Indirect Pathway

The direct and indirect pathway of movement is a neuronal circuit within the central nervous system (CNS) through the basal ganglia (Freeze, Kravitz, Hammack, Berke, & Kreitzer, 2013; Kravitz, Tye, & Kreitzer, 2012). The main goal of the two pathways is to modulate the activity of the thalamus, which normally sends inhibitory signals to the motor cortex when it is active. Specifically, the direct pathway is to facilitate the initiation and execution of voluntary movement while the indirect pathway is to prevent unwanted muscle contractions from competing with voluntary movements.

When people are making decisions about movement, the motor cortex will send commands to the striatum. The direct pathway goes from the striatum to globus pallidus internal and the main goal is to inhibit the activation of the thalamus and take away the inhibitory signals from thalamus to the motor cortex so that the proper functioning of this direct pathway results in the natural initiation of movement (Freeze et al., 2013) (Figure 1B). The most crucial neurotransmitter helping to regulate this pathway in the background is dopamine, going from the substantia nigra to the striatum. When the substantia nigra is more active, it sends more dopamine to inhibitory neurons in the striatum heading for the globus pallidus internal. Dopamine binds at D1 receptors, leading to greater inhibition and a more active thalamus (Williams et al., 2002). Excitatory neurons also travel from the STN to the substantia nigra and excite the substantia nigra, allowing for a greater release of dopamine. For the indirect pathway, responsible for the inhibition of movement, the goal is to control the thalamus by turning up globus pallidus internal inhibition, preventing overexcitation of the motor cortex (Graybiel, 2000). By receiving the commands from motor cortex, striatum sends inhibitory signals to inhibit

the activation of globus pallidus external. Since the activation of globus pallidus external has been inhibited, it has less control of the subthalamus nucleus (STN) so that the STN gets excited and then the globus pallidus internal becomes more active. As a result, the thalamus becomes more active. As a result, the active thalamus send more inhibitory signals to motor cortex so that inhibitions happen (Figure 1A). The most crucial neurotransmitter helping to regulate these pathways in the background is dopamine, going from the substantia nigra to the striatum. Dopamine has an excitatory effect upon cells in the striatum that are part of the direct pathway. This is via D1 receptors. Dopamine has an inhibitory effect upon striatal cells associated with the indirect pathway. This is via D2 receptors. In other words, the direct pathway (which turns up motor activity) is excited by dopamine while the indirect pathway (which turns down motor activity) is inhibited.

In a typical paradigm about motor inhibition and initiation, people reactively to inhibit their behaviors by reacting to the signal of stop (e.g., stop signal or NoGo signal), which is called reactive control (Aron, 2011). More recently, researchers pointed out the proactive model of motor initiation and inhibition, such that how a subject prepares to stop an upcoming response tendencies (Aron, 2011). Proactive inhibitory control is generated according to the goals of the subject rather than by an external cue. Neuroimaging studies have localized brain regions within the fronto-basal ganglia network as a putative neural circuitry underlying motor inhibition, which includes the right inferior frontal cortex (rIFC), the dorsomedial frontal cortex (mainly pre-supplementary motor area, preSMA), STN, the striatum and the primary motor cortex (e.g., Aron et al., 2007; Aron, Robbins, & Poldrack, 2014; Bai, Mari, Vorbach, & Hallett, 2005; Kim & Lee, 2011). Recently, a study combined the Go-NoGo paradigm and the monetary incentive delay task to explore the interaction between prefrontal cognitive control system and the striatal

reward processing network regions in impulsivity. Their results suggested that increased activation in the rIFC and decreased activation in the ventral striatum during the reward anticipation were associated with successful inhibitions (Behan, Stone, & Garavan, 2015). Moreover, their behavioral data suggested that the increased accuracy to NoGo signals was associated with the slowed reaction to Go signals which indicated the proactive inhibition process. These results were consistent with the proactive inhibition model which involves the indirect neural pathway from the prefrontal cortex to caudate, and to the internal globus pallidus which then projects to the internal globus pallidus prior to its output to the thalamus (Aron, 2011).

1.3.2 Hyper-direct Pathway

More recently, researchers proposed a third pathway, the hyper-direct pathway of motor inhibition. Instead of going through striatum, hyper-direct pathway originates from the right prefrontal regions and directly connects to STN (Aron et al., 2007; Chikazoe, 2010) (Figure 1C). When inhibitory commands are sent from cortex to STN, the activated STN send active signals to the thalamus so that the thalamus send the inhibitory signals to the motor cortex. Hyper-direct pathway is fast, and reactively cancels out and inhibits a motor command, which has already been placed in motor cortex. This process is consistent with reactive motor control.

In neural imaging studies, researchers found the co-activation of rIFC and STN and their activations were stronger with faster inhibitions (Aron & Poldrack, 2006). Swann et al. (2011) suggested that deep brain stimulation of the STN can improve the performance in stop-signal task in patients with Parkinson disease and increase their activation of rIFC as well. More

recently, simultaneous fMRI and EEG data suggested the interaction between the theta power from mid-frontal cortex and probability level can predict the activation of STN in a reward learning task (Frank et al., 2015). These results gave evidence of the direct connection between the frontal region and STN as the hyper-direct pathway.

Motor control and reward processing are highly interconnected. The motor system is largely influenced by the neural circuitry of the reward-related motivational system as both systems are largely modulated by the dopaminergic input from the midbrain to basal ganglia nuclei (Wickens, 1990). The proactive direct and indirect pathway is in line with the role of motivation in motor control such that when participants are uncertain about the identity of the forthcoming stimulus, an adaptive strategy will be used to prepare for inhibition, to some extent, based on their predictions and expectations to the upcoming signals. In other words, a not-yet-initiated action has to be restrained to a certain degree, which has been framed as the proactive inhibitory control (Aron, 2011). As to the reactive control, not much work has been discussed. The right prefrontal region reactively corrects movements, by canceling out and inhibiting a motor command that has already been made (Aron et al., 2007; Chambers, Garavan, & Bellgrove, 2009; Chikazoe, 2010). Because of this role of the right prefrontal region in reactive control, I hypothesized that right prefrontal region need to work harder when subjects have a stronger motivation to make the action so that it can cancel out the improper response impulsive.

1.3.3 Beta Oscillation in Motor Control and Motivational Process

Neural oscillation is rhythmic or repetitive neural activity in the central nervous system. Neural oscillations in beta frequency band (15-30 Hz) across the cortico-basal ganglia network,

especially the sensorimotor cortex and prefrontal cortex, have been widely studied in motor control. Studies have shown that patterns of motor beta oscillations code for different movement parameters modulating the initiation and inhibition of movement (see review Jenkinson & Brown, 2011). While decrease in beta band oscillations (desynchronization) initiates a movement, increase in beta oscillations (synchronization) suppresses a movement (Kühn et al., 2004; Picazio et al., 2014; Swann et al., 2012; Swann et al., 2011; Swann et al., 2009; Tan et al., 2015). To date, significance of the motor beta oscillations has mostly been studied in the context of lower level motor control focusing on how this neural signal encodes the kinematic properties of a movement (Brittain & Brown, 2014; Jenkinson & Brown, 2011; Kilavik, Zaepffel, Brovelli, MacKay, & Riehle, 2013). Only a handful of studies have started investigating their contribution in the influence of higher-level decision processes, such as the effects of reward and risk level in motor related decisions.

There are a few studies suggesting some evidence that people's motivational status could be reflected by the beta oscillation. Studies in clinical population such as patients with Parkinson's disease showed that loss of dopaminergic inputs to the striatum and leads to impairments in motivation and learning from feedback (Foerde, Braun, Higgins, & Shohamy, 2014). Dopaminergic modulations have also demonstrated these apposing effects of beta oscillations in motor initiation and inhibition (Gatev, Darbin, & Wichmann, 2006; Hammond, Bergman, & Brown, 2007). The dopamine loss in Parkinsonism elevated the level of beta frequency oscillations causing difficulty in initiating a movement, which could be mitigated by dopaminergic medications (Gatev et al., 2006). One recent study investigated how reward level can change people's motivation of making effort to motion through beta oscillation (Meyniel & Pessiglione, 2014). The participants were asked to apply motor effort in order to gain rewards

and were allowed to adjust their own effort allocation by having a break or applying greater force in order to gain as many rewards as possible. Their results showed that effort onset could be predicted by beta desynchronization during the previous break time. Moreover, the incentive reward increased movement effort measured by exerted force level through the magnitude of beta desynchronization (Myerson, Baumann, & Green, 2014). This study shed light on the relationship between reward and motor control. In addition, in a cued choice reaction task that a cue provided information as to which hand to prepare for an upcoming response, results suggested that the power of beta band decreased significantly followed by an effective cue compared to an ineffective cue indicating the role of coding the information predicting the coming motor response (Van Wijk, Daffertshofer, Roach, & Praamstra, 2008).

In sum, although some studies showed some indirect evidence of the role of coding reward information in beta band oscillation across the cortico-basal ganglia network, the underlying mechanism is still unclear. Also the neural literature has the gap of investigating the influence of risk level on motor decisions. In the current studies, the second important goal is to investigate how decision variables such as reward and risk associated with an action are coded in the beta frequency oscillations and how these cortico-basal ganglia network work together in this process.

1.4 The Present Studies

The current thesis contained two studies. Study 1 was a behavioral study aiming at developing a valid paradigm to study how reward and risk level influence people's decisions of speeded actions. A Speed-Rewarded version of the widely used Go-NoGo task was developed. In this task, participants gained or lost points based on performance speed and accuracy. The

analyses focused on how they trade-off between speed and accuracy based on different levels of potential reward and perceived risk level associated with a speeded action. The hypotheses were that there would be a systematic trade-off between speed and accuracy based on the expected value of an action, which would be calculated by potential reward and perceived risk level associated with the action.

In an effort to investigate the neural mechanism under this processing, EEG was recorded in study 2 while the participants were playing the Speed-Rewarded Go-NoGo task. Specifically, the analyses focused on the beta band (15-30 Hz) oscillation during the motor plan period and the motor reaction period and examined how the beta oscillation coded the reward and risk level in order to plan and execute the motor action through the motor pathways. The hypotheses were that the patterns of EEG motor beta oscillations would vary across the different levels of reward and risk reflecting different levels of motivation towards an action. Specifically, the level of beta oscillations would be lower when the decision variables promoted a choice towards a “Go” response (e.g. larger rewards and lower risk), whereas it would be higher when they promoted a choice for a “NoGo” (e.g., smaller rewards and higher risk).

Additionally, I am interested in whether personality traits associated with risk-taking and impulsive tendencies assessed via self-report measures, influenced the degree to which these decision variables modulated motor beta oscillations. Previous studies suggested that individuals with greater risk-taking and impulsive tendencies were less sensitive to losses and showed greater motivation towards larger compared to smaller rewards (Bechara, Dolan, & Hinds, 2002; Bornoalova et al., 2009). Therefore, I hypothesized that those individuals with greater risk-taking and impulsive tendencies would show greater changes in beta power associated with different levels of reward.

CHAPTER 2

STUDY 1: THE EFFECTS OF REWARD AND RISK LEVEL ASSOCIATED WITH SPEEDED ACTIONS: A BEHAVIORAL STUDY

2.1. Participants

A total of 110 college students (20 males, 22.21 ± 2.13 years) without a history of psychiatric and neurological illness, or alcohol/drug dependence were recruited from University of Massachusetts, Amherst, MA, United States. All study participants signed a written informed consent in accordance with the Declaration of Helsinki, approved by the UMass Institutional Review Board before the experiment and received course credits for participation after completion of the experiment.

2.2 Speed-Rewarded Go-NoGo Task

During the first phase of the task, participants completed a typical Go-NoGo task in which Go signals appeared 80% of the time in a total of 100 trials. Response times (RT) to the Go signals were used to calculate the RT categories for determining actual rewards in the Speed-Rewarded Go-NoGo task in the second phase. Five RT categories were determined based on the lognormal distribution of the Go signal RTs from the first phase (Category 1: $RT < \mu - 2\sigma$; Category 2: $\mu - 2\sigma < RT < \mu - \sigma$; Category 3: $\mu - \sigma < RT < \mu$; Category 4: $\mu < RT < \mu + \sigma$; Category 5: $RT \geq \mu + \sigma$; μ and σ refers to the mean and standard deviation of the lognormal distribution).

In the second phase of the task, participants performed the Speed-Rewarded Go-NoGo task (Fig. 2). Participants were rewarded based on the speed and accuracy of response.

Throughout the task, participants were instructed to use their right index finger to press a button on a response box. A faster response to a Go signal resulted in higher rewards, whereas an incorrect response to a NoGo signal (i.e. false alarm) was punished by loss of reward points. On each trial of the task, participants were first presented with a trial information cue. The cue contained information about the amount of reward points they could earn - either 120 (high reward) or 6 (low reward) - and the probability that a Go signal would appear in that trial as described in a pie-chart (Go-probability: 20, 50 or 80%). Following the presentation of a trial information cue, the screen displayed a "READY!" sign for a variable time window (1000-1500 msec), which prompted the participants to prepare for a response. A Go (geometric shape in blue) or NoGo (same geometric shape in gray) signal, determined by the Go signal probability, was presented in the following screen. After participant's response, the actual reward amount that the participant won based on his/her performance was displayed. A correct response to a Go signal was rewarded based on RT using the pre-defined RT category from the first phase. For trials that met the RT category 1, the total point at stake (either 120 or 6) was awarded. For trials that fall under RT category 2, 3, 4 and 5, points were discounted to 50%, 25%, 12.5% and 0% of the total point respectively. Correct responses to a NoGo signal did not result in any rewards. However, an incorrect response to a NoGo signal (i.e. false alarm) would result in a loss of the total points at stake (i.e. results in -120 or -6). Thus, the decision to Go entailed a risk for resulting in negative points. The Go-probability can therefore be considered as a metric based on which the participants can assess the risk of negative outcomes associated with the Go decision. A fixation cue was displayed during inter-trial interval. There were 6 blocks with 192 trials in total (32 trials in each block: 4 trials with low reward and 20% Go-probability; 8 trials with low reward and 50% Go-probability; 4 trials with low reward and 80% Go-probability; 4 trials with high

reward and 20% Go-probability; 8 trials with high reward and 50% Go-probability; 4 trials with high reward with 80% Go-probability). After each block, participants were shown the accumulated amount of points they've earned up until the previous block.

2.3 Behavioral Psychometric Measures

In an effort to determine how individual differences in personality traits related with impulsivity and risk taking contributes in performance during Speed-Rewarded Go-NoGo task, each participant was asked to fill the following additional scales.

Behavioral Inhibition & Activation Scale (BIS/BAS). The BIS/BAS contains 24 items and yields 4 factors measuring the behavioral inhibition system and behavioral active system (Carver & White, 1994). The four factors include Drive, Fun Seeking, Reward Responsiveness, and Behavioral Inhibition. Participants are asked to rate each item with a 4-point Likert scale.

Barratt Impulsiveness Scale (BIS). BIS is a 30 item self-report instrument designed to assess the personality/behavioral construct of impulsiveness. It has the following 3 factors: Factor 1 (motor impulsivity); Factor 2 (non-planning impulsiveness); Factor 3 (attentional impulsiveness) (Barratt, Monahan, & Steadman, 1994). Participants are asked to rate each item with a 4-point Likert scale.

Gambling Related Cognitions Scale (GRCS). GRCS contains 23 items in community-based population with five factors: Gambling expectancies, Illusion of control, Predictive control, Inability to stop gambling, and Interpretive bias (Raylu & Oei, 2004). Participants are asked to rate each item with a 7-point Likert scale.

Delay Discounting Task. The participants will choose between getting a relatively small

amount of money today or getting a relatively large amount of money in the future (Kirby, Petry, & Bickel, 1999). Here is a sample question “Would you prefer \$ 54 today, or \$ 55 in 117 days?” There were 27 items in this task. The delay discounting rate (value k) in the study was fitted to Mazur's (1987) hyperbolic equation: $V=A / (1+kD)$. This equation describes how the subjective value (V) of a reward (A) is discounted as a function of delay (D) (Mazur, 1987). High k value indicated high delay discounting rate.

2.4 Results

I analyzed the reaction time to the Go signals and the false alarm rates (the proportion of incorrect responses to NoGo signals) in each experimental condition as displayed in Table 1. Since different categories for reward size were based on the standard deviation of reaction time of each participant, Z-scored RTs were used for all the analyses. Raw RTs within each individual were log-transformed, after which they were converted into Z-scores across all the conditions.

2.4.1 The Effect of Reward and Go-Probability

A set of 2 (Reward: High, Low) x 3 (Go-probability: 20%, 50%, 80%) within subject ANOVA was performed for the RT to Go signals, the false alarm rates to NoGo signals as well as the speed-accuracy trade-off measure. For RT, there was a main effect of Reward ($F(1,99) = 27.684, p < .001, \eta^2 = .219, M_{low} = .264, M_{high} = .033$) and Probability ($F(2,198) = 88.487, p < .001, \eta^2 = .472$), as well as the interaction between Reward and Probability ($F(2, 198) = 6.572, p = .002, \eta^2 = .062$) (Fig. 3A). Post-hoc analysis suggested that when the Go-probability was relatively low (20%), there was no significant difference between RT for high reward compared

to the low reward conditions ($p = .111$). When the Go-probability was 50% and 80%, RT was significantly faster for high reward condition compared to low reward condition (both $ps < .001$, with Bonferroni correction). These results suggested that the effect of reward on speed was modulated by the assessed level of risk as described in the Go-probability. Speeding up for larger reward only happened when the Go-probability was 50% or above (i.e. when the risk for losing associated with false alarm was low).

For the false alarm rate, there was a significant main effect of Go-probability ($F(2,218) = 91.872, p < .001, \eta^2 = .457$). False alarm rate was higher in 80% probability condition ($M = .305$) than in 50% probability condition ($M = .131$), and it was higher in 50% probability condition than in 20% probability condition ($M = .054$) (all $ps < .001$, with Bonferroni correction). The main effect of reward ($F(1,109) = 2.571, p > .10, \eta^2 = .023, M_{\text{low}} = .154, M_{\text{high}} = .172$) and the interaction between reward and probability ($F(2,218) = 1.144, p > .10, \eta^2 = .010$) were not significant (Fig. 3B). These results suggest that there was a greater tendency to take risks associated with a speeded Go response when there was an explicitly known low probability for losing due to false alarm (i.e. high Go signal probability).

Whether reward and risk systematically influenced the speed-accuracy trade-off was also examined. The following formula as an index of speed-accuracy trade-off (Fitts, 1954): $1/RT * ACC$. In order to keep all the RT values positive, to be used in the speed-accuracy trade-off measure, exponential function was applied to the RT Z-scores. The higher value of the trade-off measure indicates that participants prefer to trade accuracy for faster response and the lower value means that participants prefer to trade speed for higher accuracy. The average speed-accuracy trade-off measure in different reward and Go-probability conditions was displayed in Table 1. For the speed accuracy trade-off, there was a significant main effect of reward ($F(1,88)$

= 11.261, $p = .001$, $\eta^2 = .113$) and Go-probability ($F(2,176) = 62.506$, $p < .001$, $\eta^2 = .415$) as well as the interaction between them ($F(2,176) = 5.09$, $p = .007$, $\eta^2 = .055$) (Fig. 3C). The simple effect analysis suggested that when the Go-probability was 20%, there was no significant difference between high and low reward condition ($p = .77$). When the Go-probability is 50% and 80%, the speed-accuracy trade-off was higher in high reward condition compared to low reward condition (for 50% Go-probability, $p < .001$, for 80% Go-probability, $p = .007$, with Bonferroni correction). Consistent with the results from response time, these results suggested that the effect of reward on movement speed was modulated by the assessed level of risk as described in the Go-probability. When the Go-probability was high (50% or 80%), the risk for losing associated with false alarm was low, participants preferred to trade off accuracy in order to response faster in order to get the high reward.

2.4.2 Contribution of Risk-taking and Impulsive Traits in Speed-Rewarded Go-NoGo Performance

Correlation analyses were conducted between the measures of risk-taking and impulsive traits, and the performance measures of Speed-Rewarded Go-NoGo task. The results were displayed in Table 2 and Table 3. Significantly positive correlations with the false alarm rate were found in the GRCS and delay discounting (Table 2). Significant negative correlation with the RT was found in BIS (Table 3). No significant relationships were found between speed-accuracy trade-off and any of the risk-taking and impulsive trait measures.

In general, the overall false alarm rate was positively correlated with the total score of GRCS ($r = .219$, $p = .023$, Fig. 4A). This suggested that people with higher gambling-oriented cognition style have greater tendency to take risks. Further correlation analyses were conducted

between GRCS and the false alarm rates in different reward and probability conditions. The results suggested that in the high probability condition (80%), there was a significant correlation between false alarm rate and the total score of GRCS ($r = .192, p = .046$). But in the 20% and 50% probability conditions, there were no significant correlations. Also with low reward, there was significant correlation between the false alarm rate and the total score of GRCS ($r = .255, p = .008$). But no significant correlation was found with high reward condition.

The delay-discounting rate was significantly correlated with the overall false alarm rate ($r = .241, p = .013$, Fig. 4B), indicating that individuals with larger delay discounting rate, took more risks. Across different Go signal probability conditions significant correlations were found in 20% ($r = .218, p = .024$) and 80% ($r = .229, p = .018$) probability conditions. No significant correlation was found in the 50% probability condition. Across different reward levels, in low the reward condition, there was a significant correlation between false alarm rate and delay discounting rate ($r = .256, p = .008$). No significant correlation was found with high reward condition.

There was a significant negative correlation between the RT and BIS in BIS/BAS ($r = -.199, p = .05$, Fig. 4C), indicating that individuals with greater behavioral avoidance (behavioral inhibition system) would respond faster. Further correlation analyses were conducted between BIS/BAS and the RT in different reward and probability conditions. For BIS subscale, there was not any significant correlations across different reward and Go-probability conditions. But there was a positive correlation between BAS and the RT in low reward condition ($r = .203, p = .047$). This suggested that individuals with greater behavioral approach system (behavioral activation system) would respond slower in low reward condition. But no significant correlation was found in high reward condition as well as the different Go-probability conditions.

In an effort to determine whether the relationship with the risk-taking and impulsive trait measures differently change across reward level Go-probabilities, I calculated the difference in false alarm rate between high and low reward conditions separately in each probability condition and looked at the correlation between this difference measure with the risk-taking and impulsive trait measures. The results showed that in the 20% probability condition, the difference of false alarm rate between the high and low reward conditions were negatively correlated with total score of GRCS ($r = -.281, p = .003$, Fig. 4D). With 50% and 80% probability conditions, no significant correlations were found. This indicated that the effect of reward on increasing false alarm rate was greater for people who demonstrated less gambling oriented cognition styles and that this effect was specific when the Go signal probability was low. No significant correlations were found with the delay-discounting rate and BIS/BAS.

CHAPTER 3

STUDY 2: THE EFFECTS OF REWARD AND RISK LEVEL ASSOCIATED WITH SPEEDED ACTIONS: THE ROLE OF BETA OSCILLATIONS

3.1 Participants

A total of 31 right-handed college students (26 females, 19.70 ± 1.08 yrs) without any history of psychiatric or neurological illnesses were recruited from the University of Massachusetts, Amherst. All study participants signed a written informed consent, approved by the UMass Institutional Review Board. Participants performed the Speed-Rewarded Go-NoGo task while EEG was collected continuously. Participants received course credits for participation after completion of the experiment. In addition to the flat rate of credit for participation itself, an extra bonus credit – 25% of the flat rate – was granted based on the reward points they earned throughout the Speed-Rewarded Go-NoGo task.

3.2 Speed-Rewarded Go-NoGo Task

The participants performed same task as Study 1. There were six blocks with 288 trials in total (48 trials in each block with 8 trials per each reward level and Go-probability combination). After each block, participants were shown the accumulated amount of points they've earned up until the previous block.

3.3 EEG Recording and Analysis

The electroencephalogram (EEG) was continuously recorded using 64 scalp electrodes embedded in an extended coverage, triangulated equidistant cap (M10, EasyCap, GmbH) using a

low-pass filter of 100 Hz at a sampling rate of 1000 Hz (actiCHamp, Brain Products, GmbH). The electro-oculogram (EOG) was monitored with electrodes below the left eye and just lateral to the left and right canthi. Electrode impedances were kept below 25 k Ω . The EEG was amplified with a BrainAmp system (Brain Products GmbH, Gilching, Germany). All channels were referenced to the vertex (Cz) during recording.

Offline EEG data were exported to Matlab using the EEGLAB software package (Delorme & Makeig, 2004), and custom scripts. The data were re-referenced to the average of mastoid channels and high-pass filtered by 0.1 Hz. Then I separated the remaining data into two epochs. First epoch was time-locked to the presentation of the trial information, spanning from 1 s prior to and 4.5 s after the onset of the trial information. This epoch includes the 2.5 s *Trial Information period* as well as the 2 s of *Ready period*. These two periods share the same baseline which was 1 s duration before the onset of trial information. The second epoch was time-locked to the presentation of the Go/NoGo signal, spanning from 200 ms prior to and 800 ms after the onset of the Go/NoGo signal (*Go/NoGo period*). A pre-stimulus period of 200 ms was used as the baseline. For each participant, artifact noise was removed based on an independent component analysis (ICA) approach (Delorme, Palmer, Onton, Oostenveld, & Makeig, 2012; Makeig, Debener, Onton, & Delorme, 2004; Onton & Makeig, 2006) that has been established previously to obtain EEG data, which greatly diminished contribution from ocular/biophysical artifacts. Single trials were also visually inspected to exclude epochs with excessively noisy EEG or muscle artifacts.

Time-frequency analysis of the EEG data was performed using the *timef* function of the EEGLAB toolbox (Delorme & Makeig, 2004). Oscillatory power in beta band was calculated by means of Fast Fourier Transformation and the mean event-related (log) spectral perturbation

(ERSP) was computed with respect to the specific pre-stimulus period as baseline (i.e. -1000 to 0 ms for Trial Information and Ready period and -200 to 0 ms for Go/NoGo signal period). The epoch became -488 ms to 3988 ms for the Trial Information and Ready period and -136 ms to 736 ms for Go/NoGo signal period.

The analyses focused on the pre-selected electrodes relevant to the proactive and reactive motor control. Specifically, these electrodes of interest encompass the left primary motor region contralateral to the right hand used for the response (C3, C5, CP3, CP5) (Deiber et al., 2012) and the right prefrontal region (F6, F8, FC6) (Swann et al., 2011). Signals from all of the electrodes were averaged within the motor and right frontal regions as in previous literature (Deiber et al., 2012; Swann et al., 2011). Statistical analyses were performed separately in the following three periods; Trial Information, Ready and the Go/NoGo period on mean ERSP values in beta frequency band. In order to determine the time window that shows significant effects associated with reward and risk level, a point-by-point 2 (Reward: High, Low) x 3 (Go-probability: 25%, 50%, 75%) repeated measures ANOVA was performed within each period. After the specific time windows were determined, statistics were reported based on the average across all time points within the identified time window.

3.4 Behavior Psychometric Measures

Based on the results in study 1, the change of behavioral performance between high and low reward condition was only predicted by GRCS. Therefore, in study 2, only GRCS was measured as the personality traits related with risk-taking and impulsive tendencies.

3.5 Results

3.5.1 Behavioral Results

The reaction time and the false alarm rates (the proportion of incorrect responses to NoGo signals) were analyzed in each experimental condition. Since different categories for the actual reward size were based on the standard deviation of the reaction times, Z-scored RTs were used for all the analyses as in study1 (X.-J. Chen & Kwak, 2017). Raw RTs within each individual were log-transformed, after which they were converted into Z-scores.

A set of 2 (Reward: High, Low) x 3 (Go-probability: 25%, 50%, 75%) repeated measures ANOVA for the RT to Go signals and the false alarm rate to NoGo signals were performed to determine how reward and Go-probability influence behavioral performance. For RT, there was a main effect of Reward ($F(1,30) = 53.15, p < .001, \eta^2 = .64, M_{\text{low}} = .34, M_{\text{high}} = -.03$) and Go-probability ($F(2,60) = 43.62, p < .001, \eta^2 = .59, M_{25} = .38, M_{50} = .19, M_{75} = -.13$), as well as the interaction between Reward and Go-probability ($F(2,60) = 14.44, p < .001, \eta^2 = .33$) (Fig. 5A). Pairwise comparisons suggested that across the three levels of Go-probability (25%, 50%, 75%), RT was significantly faster for high reward compared to low reward condition (25% Go-probability, $p = .016$, 50% and 75% Go probability: both p values $< .001$, with Sidak Bonferroni correction). These results suggest that the effect of reward on speed was modulated by the assessed level of risk as described in the Go-probability. Speeding up for larger reward only happened as the Go-probability increased (i.e. when the risk for losing associated with false alarm decreased).

For the false alarm rate, there was a significant main effect of Go-probability ($F(2,60) = 32.73, p < .001, \eta^2 = .52, M_{25} = .04, M_{50} = .11, M_{75} = .26$) (Fig. 5B). False alarm rate was higher in 75% than in 50% Go-probability, and in 50% than in 25% Go-probability (all p values $< .001$).

The main effect of Reward ($F(1,30) < 1, p = .390, M_{\text{low}} = .13, M_{\text{high}} = .14$) and the interaction between Reward and Go-probability ($F(2,60) < 1, p = .381$) were not significant. These results suggest that there was a greater tendency to take risks associated with a speeded Go response when the probability of losing was lower (i.e. higher Go-probability).

The analysis also examined whether reward and risk systematically influenced the speed–accuracy trade-off using the following formula as an index of speed–accuracy trade-off: $1/RT \times ACC$ as in the previous study (Chen & Kwak, 2017). In order to keep all the RT values positive to be used in the speed–accuracy trade-off measure, exponential function was applied to the RT Z-scores. The higher value of the trade-off measure indicates greater preference to trade accuracy for faster response and the lower value indicates greater preference to trade speed for higher accuracy. Reward by Go-probability repeated measures ANOVA showed a significant main effect of reward ($F(1,30) = 34.31, p < .001, \eta^2 = .53, M_{\text{low}} = .47, M_{\text{high}} = .62$) and the interaction between them ($F(2,60) = 5.66, p = .006, \eta^2 = .16$) (Fig. 5C), suggesting a systematic trade-off between reward and risk level on decisions for speeded actions. Participants showed a greater tendency to go faster at the expense of sacrificing the accuracy as the reward stakes increased. This effect of reward magnitude was more significant in higher than lower Go-probabilities ($p = .013$ when Go-probability = 25%, $p = .001$ when Go-probability = 50%, $p < .001$ when Go-probability = 75%, with Sidak Bonferroni correction). The main effect of Go-probability was not significant ($F(2,60) < 1, p = .581$).

Next, I determined whether the task performance predicts individual's risk-taking and impulsive tendencies. Based on prior studies suggesting greater sensitivity to reward magnitudes associated with risk-taking and impulsive tendencies (Bechara, Dolan, & Hines, 2002; Bornoalova et al., 2009), the analysis was focused on the effect of reward magnitude. To this

end, I computed the difference in false alarm rate and RT as well as the speed-accuracy trade-off measure between high and low reward conditions averaged across the three Go-probabilities and looked at the correlation between this difference measure and self-report psychometric measures. Difference in false alarm rate across high and low reward conditions was positively correlated with Gambling Expectation sub-score ($r = .517, p = .003$) and the total score ($r = .378, p = .036$) of GRCS. Overall the behavioral findings were consistent with the study1 (Chen & Kwak, 2017).

3.5.2 EEG results

3.5.2.1 EEG beta band activity during Trial Information and Ready Period

During Trial Information Period, time frequency map from both the left sensorimotor and right frontal regions showed a marked decrease in beta power after the onset of the Trial Information cue lasting until about 1500 ms (Fig. 6 A and B, Fig. 7 A and B). Thus, the analysis was focused within this time period for both regions. In the left sensorimotor region, point-by-point 2 (Reward: High, Low) x 3 (Go-probability: 25%, 50%, 75%) repeated measures ANOVA showed a significant main effect of Reward from 645 ms to 1195 ms after the onset of Trial Information cue ($F(1,30) = 11.21, p = .002, \eta^2 = .27, M_{\text{low}} = -0.22, M_{\text{high}} = -0.30$, Fig. 6C) and a significant main effect of Go-probability between 400-1175 ms after the onset of Trial Information cue ($F(1,60) = 11.04, p < .001, \eta^2 = .27, M_{25} = -0.27, M_{50} = -0.29, M_{75} = -0.52$, Fig. 6D). Post-hoc analysis suggested that the difference between 25% and 50% Go-probability condition was not significant ($p = .768$) whereas the beta power in 75% Go-probability condition was significantly lower than the other two conditions (both p values $< .001$). No significant interaction was found during Trial Information period.

Similar pattern was found in the right prefrontal region during Trial Information Period. Point-by-point 2 (Reward: High, Low) x 3 (Go-probability: 25%, 50%, 75%) repeated measures ANOVA showed a main effect of Reward between 765-1005 ms after the onset of Trial Information cue ($F(1,30) = 4.86, p = .035, \eta^2 = .14, M_{\text{low}} = -0.12, M_{\text{high}} = -0.22$, Fig. 7C) and a main effect of Go-probability was found between 905-1275 ms after the onset of Trial Information cue ($F(1,60) = 5.27, p = .008, \eta^2 = .15, M_{25} = -0.10, M_{50} = -0.07, M_{75} = -0.23$) (Fig. 7D). Post-hoc analysis suggested that beta power in 75% Go-probability condition was significantly lower than the 25% ($p = .018$) and 50% Go-probability condition ($p = .008$).

During Ready Period, time frequency maps from the left sensorimotor and right frontal regions showed a marked decrease in beta power across the entire period which lasts 1500 ms (Fig. 6 A and B, Fig. 7 A and B). Thus the analysis was performed across the whole period. In left sensorimotor region, point-by-point 2 (Reward: High, Low) x 3 (Go-probability: 25%, 50%, 75%) repeated measures ANOVA only showed a main effect of Go-probability between 275-495 ms after the Ready onset ($F(1, 60) = 3.32, p = .043, \eta^2 = .10, M_{25} = -0.43, M_{50} = -0.46, M_{75} = -0.62$, Fig. 6E). Post hoc analysis suggested that the beta power with 75% Go-probability was significantly lower compared to the 25% Go-probability condition ($p = .024$). The difference between 25% and 50% Go-probability conditions ($p = .653$) as well as the difference between 50% and 75% Go-probability conditions ($p = .063$) were not significant. No significant main effect of Reward or interaction were found. In the right prefrontal region, there was a significant main effect of Reward between 1185-1420 ms after the onset of Ready ($F(1,30) = 5.10, p = .031, \eta^2 = .15, M_{\text{low}} = -0.16, M_{\text{high}} = -0.27$, Fig. 7E). The main effect of Go-probability and the interaction were not significant.

3.5.2.2 EEG beta band activity during Go/NoGo period

The trials in Go/NoGo period could further be divided into trials when a Go signal was presented (Go trials) and trials when a NoGo signal was presented (NoGo trials). Previous literature suggested that beta power was modulated by efforts placed for motor inhibition (Swann et al., 2009, 2011; Wagner, Wessel, Ghahremani, & Aron, 2017). Based on these reports, I computed the difference in mean beta power between the two trial types (beta power_{NoGo - Go}; beta power in NoGo trials – beta power in Go trials) and determined whether there was a modulation by Reward and Go-probability in this difference measure. The greater the value in this difference measure would reflect greater effort placed for adequate motor inhibition. Thus, I interpreted this measure as metric of inhibitory motor effort. I hypothesized that in general, if the Trial Information led to a greater motivation towards a Go response, it would require a greater inhibitory effort in face of an actual NoGo signal and thus beta power_{NoGo - Go} will be higher. In the analysis, trials with only correct responses were included, excluding the false alarms trials and the missed trials where no responses were made to the Go signal. In determining the specific time period for analysis, the common time window prior to the actual Go response across all participants to account for individual differences in RT was investigated. Specifically, the first 200 ms from the onset of the Go/NoGo signal, which was the minimum average RT across all participants, was analyzed.

In order to examine how Reward and Go-probability modulated beta power_{NoGo - Go} in left motor region, initial inspection of the results revealed no specific time point at which the patterns of beta frequency power were distinguishable across the Reward and Go-probability conditions. 2 (Reward: high, low) x 3 (Go-probability: 25%, 50%, 75%) repeated measures ANOVA did not show any main or interaction effects.

As opposed to the left motor region, there was a marked difference in the patterns of beta frequency power in the right frontal region. Point-by-point 2 (Reward: high, low) x 3 (Go-probability: 25%, 50%, 75%) repeated measures ANOVA showed a significant main effect of Reward between 110-135 ms after the onset of the Go/NoGo signal ($F(1,30) = 5.29, p = .029, \eta^2 = .15, M_{\text{low}} = -0.24, M_{\text{high}} = 0.23$, Fig. 8B). Furthermore, a significant Reward by Go-probability interaction was found between 135-160 ms after the onset of the Go/NoGo signal ($F(2,60) = 3.40, p = .040, \eta^2 = .10$, Fig. 8A, C). Post-hoc analysis showed that in 75% Go-probability condition, beta power $_{\text{NoGo} - \text{Go}}$ was significantly greater in high compared to low reward condition ($p = .038$, with Sidak Bonferroni correction) while in 25% and 50% Go-probability condition, there was no significant difference between high and low reward condition (both p values $> .05$). No significant main effect of Go-probability was found.

3.5.2.3 EEG Beta band activity predict performance on Speed-Rewarded Go/NoGo task

In order to determine whether the beta frequency oscillations in the left motor and right frontal regions influenced behavioral performance to the forthcoming Go/NoGo signal, linear mixed effect model was used. I hypothesized that the difference in behavioral performance (i.e. FA and RT) across Reward and Go-probability conditions will be predicted by difference in beta power across these conditions. To simplify our interpretations, a model that predicts the difference in performance across the high and low reward conditions from the difference in beta oscillations across the two reward conditions was created below.

$$Performdiff_{ij} = \beta_1 Prob_j + \beta_2 Betadiff_{ij} + \beta_3 Prob_j \times Betadiff_{ij} + \gamma_1 Prob_j + \epsilon_{ij} \quad (i = \text{subject } i, j = \text{Go-probability } j, \epsilon = \text{error term})$$

Difference in response time (RT), false alarm rate (FA) and speed-accuracy tradeoff (SA) across the high and low reward conditions (*Performdiff*: high – low RT (RT_{diff}), high – low FA (FA_{diff}), high – low SA (SA_{diff})) were the dependent variables for each model. Go-probability (*Prob*), difference in beta power across high and low reward conditions (*Betadiff*: high – low beta power) and the interaction between the two (*Prob* x *Betadiff*) were included as fixed-effect variables predicting *Performdiff*. Go-probability was included in the model to account for the fact that each subject had its own set of random parameters associated with the random effect “Prob” ($\gamma_1 Prob_j$). Separate models were tested for *Betadiff* derived from motor and right frontal regions in the Trial Information, Ready and Go/NoGo period. Mean beta power was extracted from the time window that showed significant effects associated with Reward. As for the Go/NoGo period, *Betadiff* was computed using the derived metric of inhibitory motor effort (beta power_{NoGo – Go}). Only significant results were reported below.

During Ready period, there was a significant interaction between *Betadiff* in right frontal region and Go-probability in predicting FA_{diff} ($F(2,64.9) = 4.85, p = .01$). Reward-associated increase in FA was predicted by reward-associated decrease in beta power, most reliably in 50% Go-probability (see Fig. 9A). During the Go/NoGo period, there was a significant main effect of *Betadiff* ($F(1,71.00) = 4.32, p = .041$) and an interaction between *Betadiff* and Go-probability ($F(2,51.37) = 3.51, p = .037$) in the right frontal region. Increase in FA was predicted by lower levels of inhibitory motor efforts most reliably in 75% Go-probability (see Fig. 9B).

3.5.2.4 Beta Oscillation predicts individual difference in risk-taking and impulsive tendencies.

Correlation analyses were conducted to test if the beta power from left sensorimotor and right prefrontal region can predict individual's risk taking and impulsive tendencies. I hypothesized that people with stronger risk taking and impulsive tendencies would be more sensitive to reward magnitudes reflected by the difference in beta power across the high and low reward conditions. In the analysis investigating the relationship between the psychometric measures and the behavioral performance (i.e. RT, FA and SA during Speed-Rewarded Go/NoGo task), the results with the Gambling Expectation subscore and the total score of GRCS as reported earlier were significant. Thus, only these two psychometric measures (PsychM) were included in the analyses. Similar to the correlation analyses between the psychometric measures and behavioral performance, I calculated the difference beta power between high and low reward conditions and averaged them across the three Go-probabilities.

During the Trial Information period, there was a significant negative correlation between Gambling Expectation sub-score and the difference beta power in left sensorimotor region ($r = .52, p = .003$, Fig. 9C). Similar pattern was found in right prefrontal region during the Ready period, there was a negative correlation between $\text{Beta}_{\text{diff}}$ and Go-probability and Gambling Expectation sub-score ($r = .40, p = .026$, Fig. 9D).

CHAPTER 4

DISCUSSION

The two studies in the current thesis aimed to explore the effect of reward and risk on decisions for speeded actions and the underlying neural bases.

In Chapter 2, I described a task paradigm designed to investigate how decision making for speeded motor responses can vary across different levels of the potential rewards and risks. In this task, faster responses would result in higher rewards while at the same time it also entailed a higher risk of losing rewards due to false alarm. The behavioral results showed that higher rewards motivated people to respond faster, and this effect was modulated by the Go-probability which explicitly influenced the perceived risk associated with the action. Specifically, when the probability of Go signals was relatively high (the perceived risk level was low), the higher rewards led to significantly faster response to Go signals whereas the modulatory effect of reward was not significant when the probability of Go signals was low. More importantly as shown by the results of the speed-accuracy trade-off measure, there was a greater sacrifice for accuracy in favor of speed when the response was associated with higher potential reward and when the perceived risk level was low (i.e. higher Go-probability). These results suggest that decisions for a speeded action is determined by a systematic trade-off between cost and benefit associated with an action, which is based on the potential reward and risk level, the two determinants of the action value.

These results were in line with previous studies showing the powerful motivational role of monetary rewards in the conscious selection of actions (Ballanger et al., 2006; Kurniawan et al., 2010; Meyniel & Pessiglione, 2014; Skvortsova et al., 2014). In the present study, the level

of potential rewards was presented as either high or low and the actual amount of reward was proportionally deducted from the potential reward based on the speed of the response. As expected, higher rewards resulted in faster responses suggesting an increase in motivation. Faster responses, however is inevitably associated with higher risk of incorrect responses as generally depicted in speed-accuracy trade-off (Fitts, 1954), which is readily acknowledged in our everyday decision making as implied in the idiom “Haste makes waste”. In the task, the risk associated with speed was formalized by imposing a loss of points when there was a false alarm, a feature that adds on an ecological validity to the task. The results showed that decisions on speeded actions were also made based on the potential rewards to gain as well as the associated risk level similar to the way economic choices are made. Specifically, as preparing for a faster response introduces higher risk of failure to inhibit the action which may result in loss of points, participants only decided to speed up when the known probability of losing is low (i.e. higher Go signal probability).

In Chapter 3, I described how motor beta frequency oscillations were modulated by the different levels of rewards and risks. Analysis of neural signals from EEG data focused on the beta frequency oscillations involved in motor control. Specifically, the analyses focused on the sensorimotor and right frontal regions each representing the neural circuitry of proactive and reactive motor control (Aron, 2011). While EEG has low spatial resolution and it is difficult to map out the neuroanatomical origins of the EEG signal, many studies have reliably interpreted the EEG beta oscillations close to the primary motor cortex (e.g. C3, C5, CP3, CP5) as the sensorimotor rhythm (Deiber et al., 2012; López-Larraz et al., 2015; Picazio et al., 2014). EEG beta signal from the right frontal region has also been well identified as reflecting the activity of the reactive stopping network (Swann et al., 2011). Consistent with behavioral results, motor

beta oscillations reflected the differential levels of motivation towards a Go vs. NoGo response across different reward and risk levels. In general, lower beta power was associated with higher reward and lower risk level, which was consistent with prior research showing decrease in beta oscillations associated with initiating a movement and increase in beta oscillations associated with inhibiting a movement (Kuhn et al., 2004; Picazio et al., 2014; Swann et al., 2011, 2009; Tan et al., 2015). Functional relevance of these beta signals in task performance also supports this interpretation; greater reward-related decrease in beta oscillations in the right frontal region during ready period predicted greater reward-related increase in false alarm rate.

One advantage of EEG is allowing investigation of the dynamic changes of a psychological process. The Speed-Rewarded task were divided into three phases including the Trial Information period, Ready period and the Go/NoGo period in order to examine how individuals preprocess the information cue, prepare the motor actions and react to the actual motor signals. During the Trial Information period, comparisons of the EEG data across different reward and risk levels suggested that the motor beta oscillations coded the reward and risk level information. With greater amount of reward points, people showed more decrease of beta power from the sensorimotor cortex. Similarly, with higher possibility to a Go signal, people also showed more decrease of beta power in sensorimotor cortex. Same patterns happened in the right prefrontal region during this period. The current data demonstrate that beta oscillation contributes in processing higher-level decision variables such as the risk and rewards associated with an action. The involvement of both sensorimotor and prefrontal region gave evidence of proactive role of the “stopping network” happened during the Trial Information process. During the Ready period, there was a significant effect of Reward on the beta band oscillatory activity from right prefrontal region but not in sensorimotor cortex. Significant effect of Go-probability

was only found in left sensorimotor cortex, which was consistent with previous studies that the power of beta band decreased significantly followed by an effective cue compared to an ineffective cue (Van Wijk et al., 2008) indicating the role of coding the information predicting the coming motor response.

It was also of note that even within the preparatory periods when participants processed *Trial Information* and gets *Ready* for the upcoming signal, I observed distinct contributions of the two brain regions. While both reward and risk information were coded in both regions during Trial Information period, the two variables were separately coded by the two regions by Ready period with risk information in the motor region and reward information in the right frontal region. The reward information, which entails direct motivational value towards a Go response, is constantly being monitored by the reactive control system so that when necessary – for example when facing an actual NoGo signal – it can appropriately inhibit responses. The risk information, which is expressed as Go-probabilities in the current paradigm, can be more intuitively coded by the proactive mechanism in motor region as it plans out a motor command based on the degree to which the Go signal is expected.

More interesting, the beta oscillation could also predict individual differences in risk-taking and impulsive tendencies as assessed by self-report measures. During Trial Information period, individuals with greater pro-gambling cognitive orientation, measured by Gambling Related Cognition Scale (GRCS) (Raylu & Oei, 2004) showed greater decrease in beta power in the sensorimotor cortex in high compared to low reward stakes. This provides the neural evidence indicating that individuals with greater pro-gambling cognitive tendencies are not capable of adequately adjusting their behaviors in response to high stakes of reward especially during the earlier Trial Information processing period. They have greater motivation towards

larger rewards and at the same time have less sufficient inhibitory control mechanism in place which is often reported as a hallmark of impulsivity (Beck et al., 2009; Martin & Potts, 2004; Scheres, Milham, Knutson, & Castellanos, 2007). But the beta oscillation during Trial Information period could not predict any behavioral performance in the Speeded-Reward Go-NoGo task. While during the Ready period, in addition to predicting individual difference in risk taking and impulsive tendencies, the change of beta power between high and low reward conditions from right prefrontal region can also effectively predict the later false alarm rate in Speed-Rewarded Go/NoGo task. These results confirm the proactive role of prefrontal cortex that during the Ready period, the prefrontal regions may play a role of motor plan based on the Trial Information and suggested the proactive control from prefrontal lobe in motor inhibition (Aron, 2011; Aron et al., 2007). Future studies are required to directly specify the separable contributions of the two control mechanisms in processing reward and risk information to confirm these hypotheses.

As previous literature suggested, the right prefrontal region reactively corrects movements, by canceling out and inhibiting a motor command that has already been made (Aron et al., 2007; Chambers, Garavan, & Bellgrove, 2009; Chikazoe, 2010). Because of this role of the right prefrontal region in reactive control, I hypothesized that the modulatory effects of the different reward and Go-probability conditions would primarily be found after the Go/NoGo signal. Specifically, when facing an actual NoGo signal, the load that was placed in this region to inhibit a response would be greater when there was a greater motivation to “Go” based on the Trial Information. Thus, I hypothesized that the beta signals in the right prefrontal regions would manifest a greater effort to inhibit when the expected values for a “Go” response was higher as indicated during Trial Information period. The data supported this hypothesis. The inhibitory

effort – indexed by beta power $_{NoGo-Go}$ – was higher for high stakes compared to low stakes. And main effect of reward was modulated by the Go-probability condition. Specifically, greater inhibitory effort was made for high reward compared to low reward with 75% Go-probability, whereas no such difference was found with 50% or 25% Go-probability. More importantly, the beta signals predicted behavioral performance to the Go/NoGo signal. These results collectively demonstrate that the decision variable such as reward value and the risk level can shape the motor system by modulating the neural oscillation patterns involved in the proactive and reactive control, which guides a motor response.

Literature on beta frequency oscillations across the cortico-basal ganglia network suggests that different information is represented in this neural signal. With regards to the sensorimotor beta rhythm, it is suggested that it codes estimation of time towards an action (Arnal, 2012; Fujioka, Trainor, Large, & Ross, 2012), general movement planning (Engel & Fries, 2010; Jenkinson & Brown, 2011) or an anticipatory up-regulation of motor processing in face of an upcoming action (Bai et al., 2005; Kilavik et al., 2013). Furthermore, it is also associated with inhibiting an action (Swann et al., 2011; Swann et al., 2009; Wagner, Wessel, Ghahremani, & Aron, 2018). In addition to the sensorimotor rhythm, beta oscillations are also widely reported from prefrontal regions while processing rewards. Both anticipation (Kawasaki & Yamaguchi, 2013) and delivery (Cohen & Ranganath, 2007; HajiHosseini, Rodríguez-Fornells, & Marco-Pallarés, 2012) of rewards increased beta oscillations in frontal regions during reward learning and risky gambling tasks. More recent line of work has demonstrated that reward-related signals are also present in the sensorimotor rhythm (Meyniel & Pessiglione, 2014). Presentation of larger compared to smaller prospective reward resulted in greater motivation to exert physical force towards obtaining the reward, which was reflected as greater

desynchronization of the beta rhythm from the sensorimotor region. These results support the role of sensorimotor beta rhythm in translating the motivation towards a motor activation. The results extend these findings showing how both reward magnitude and risk level shape the pattern of sensorimotor rhythm to guide the upcoming action. My claims are strongly supported by the data showing direct contribution of beta oscillations in predicting individual differences in behavioral task performance as well as impulsive and risk-taking tendencies measured through GRCS.

There were several limitations in the present studies. First, our sample was limited to undergraduate college students. The current results could not be generalized to the general population. Further studies should recruit a large sample size with a wider age range from the community. Second, there was a great gender bias in the present samples with much more female compared to the male participants. Previous literature suggested the gender difference in inhibitory control (e.g., Li, Huang, Constable, & Sinha, 2006). Further studies are required to clarify the effect of gender with more balanced sample size between males and females. Finally, due to the poor spatial resolution of EEG, it is hard to determine the specific brain regions actually work together during the decision making process of speeded actions. For future study, it is important to combine multiple neural measurements such as fMRI for a better understanding of the neural mechanism of this process.

In sum, the present studies investigated the contribution of the reward amount and assessed risk level in decision making for speeded actions and the neural correlates of this process. A novel experimental paradigm presenting an ecologically valid decision making scenario, which implements both reward and risk during a Go-NoGo task was used in the present studies. The results indicate that in general, larger rewards increases movement speed despite

being associated with higher risk of losing and the degree to which reward influences performance, is modulated by the assessed risk-level. This is reflected as a systematic speed-accuracy trade-off across different levels of reward and risk, which are the two determinants of the action value. At the neural level, the beta frequency oscillations from sensorimotor cortex and the right prefrontal region represent the reward magnitude and risk level in order to guide decision making. Moreover, individual differences in risk taking and impulsive tendencies contributes to this process such that individuals with greater risk taking and impulsive tendencies does not adequately adjust their behavior across different reward levels. The results demonstrate that when making decisions for a speeded action, the associated costs and benefits are evaluated based on the potential reward and risk level, which are the two determinants of the action value. In addition, these decision variables can guide choice for actions by modulating brain oscillations.

Table 1: Performance of Speed-Rewarded Go-NoGo task in each condition

		20%		50%		80%	
		M	SD	M	SD	M	SD
Low reward	FA for NoGo	0.056	0.097	0.112	0.124	0.294	0.304
	Z-scored RT for Go	0.465	0.520	0.290	0.424	0.026	0.512
	Speed-accuracy trade-off	0.783	0.504	0.951	0.500	1.806	1.86
High reward	FA for NoGo	0.052	0.071	0.149	0.156	0.316	0.289
	Z-scored RT for Go	0.348	0.454	0.073	0.234	- 0.314	0.321
	Speed-accuracy trade-off	0.862	0.650	1.200	0.572	2.399	1.875

Note. FA: false alarm rate; RT: reaction time

Table 2: The correlations among false alarm rate, delay discounting rate and impulsive and risk-taking tendencies in each probability and reward condition

	BIS/BAS		Barratt Impulsiveness Scale	GRCS	Delay Discounting Rate (k)
	BIS	BAS			
FA_20	-.025	.102	-.089	.177	.218*
FA_50	-.005	-.094	-.118	.15	.117
FA_80	-.012	.013	-.025	.192*	.229*
FA_Low	.022	.011	-.097	.255**	.256**
FA_High	-.045	-.021	-.04	.143	.177
FA_Total	-.015	-.007	-.076	.219*	.241*

Note. * $p < .05$

** $p < .01$

FA_20; FA_50; FA_80: False alarm rate in 20%, 50%, 80% Go-probability conditions, FA_Low; FA_High: False alarm rate in high and low reward conditions, FA_Total: overall false alarm rate.

Table 3: The correlations among normalized RT, discounting rate and risk preference in each probability and reward condition

	BIS/BAS		Barratt Impulsiveness Scale	GRCS	Delay Discounting Rate (k)
	BIS	BAS			
Z-scored RT_20	-.067	.09	-.001	-.085	.125
Z-scored RT_50	-.119	.076	-.11	.061	.125
Z-scored RT_80	-.099	.126	-.029	-.093	-.077
Z-scored RT_Low	-.184	.203*	-.139	-.08	.04
Z-scored RT_High	.035	-.111	.105	.078	.125
Z-scored RT_Total	-.199*	.177	-.101	-.129	.103

Note. * $p < .05$

** $p < .01$

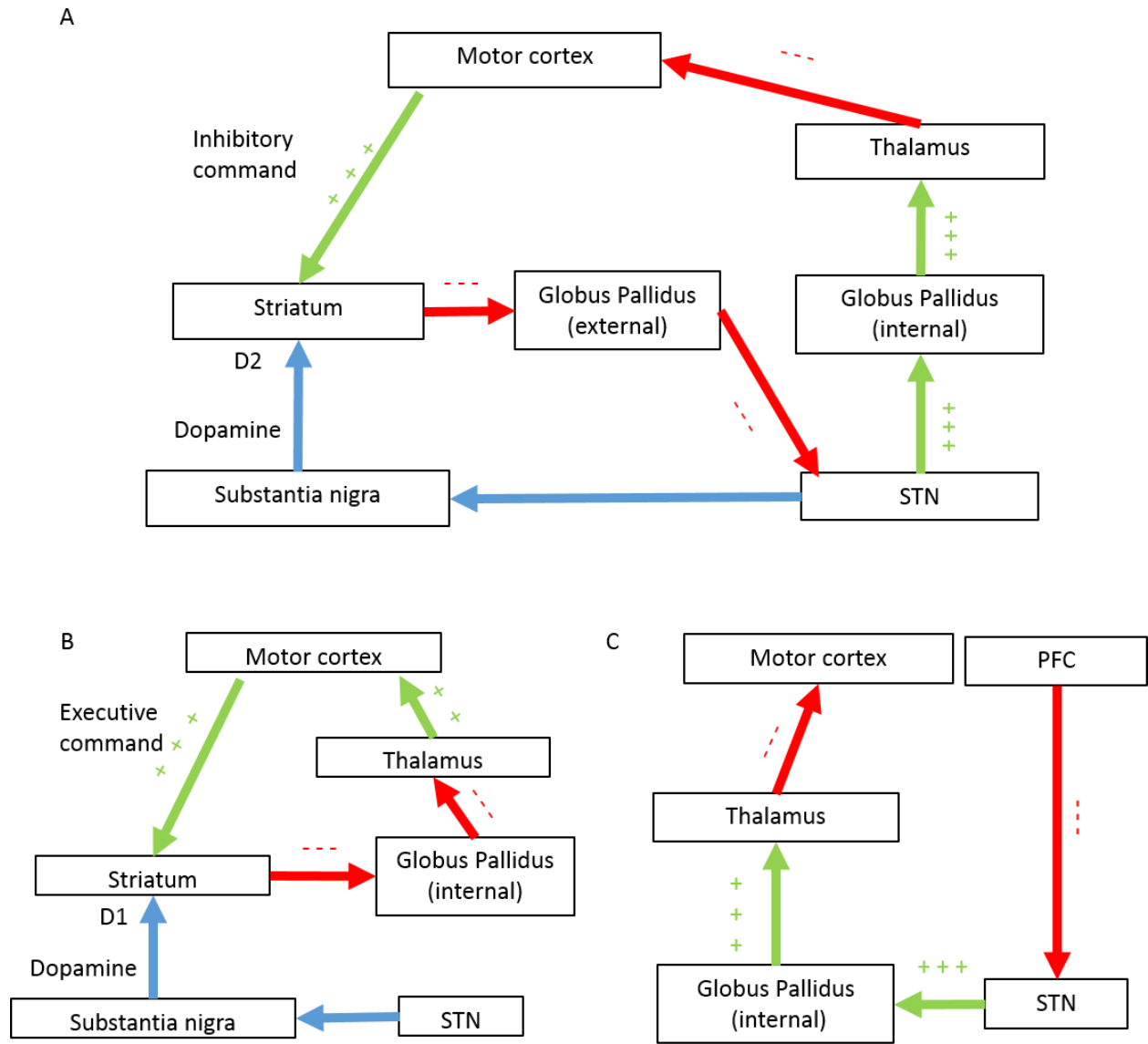


Figure 1: The motor pathways. A) Indirect pathway; B) Direct pathway; C) Hyper-direct pathway.

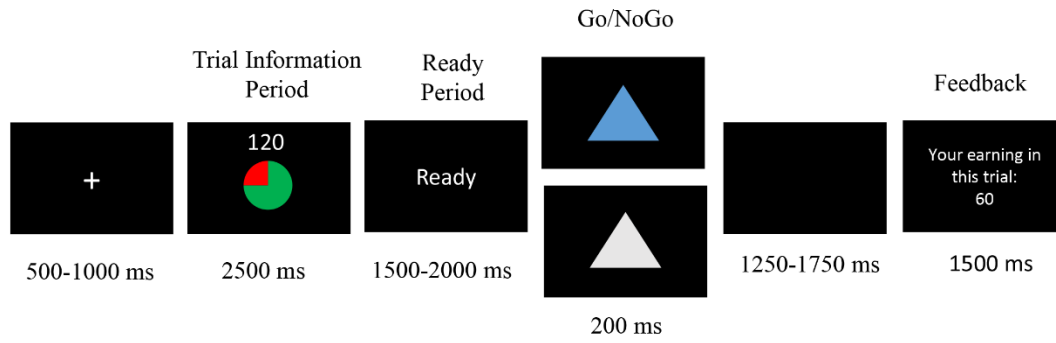


Figure 2: The trial structure of Speed-Rewarded Go-NoGo task.

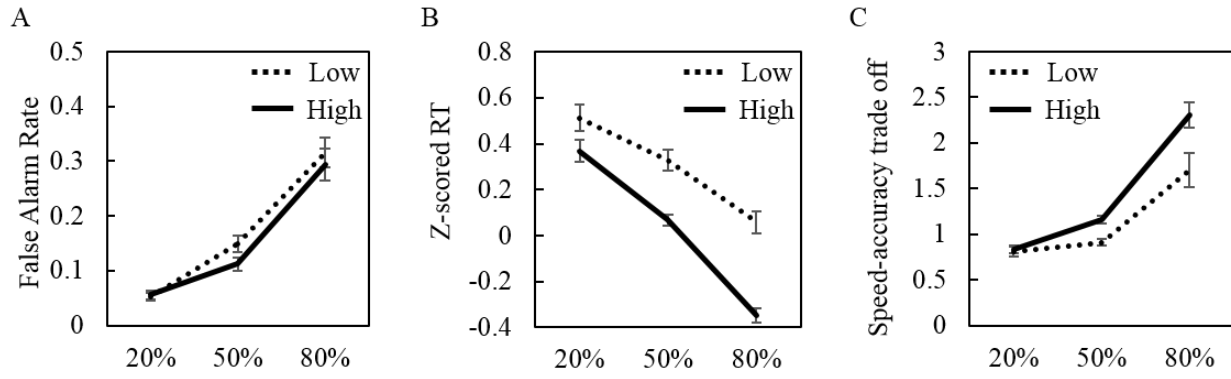


Figure 3: The performance of Speed-Rewarded Go-NoGo task (study1). (A) Z-scored RT; (B) false alarm rate; (C) the speed-accuracy trade-off.

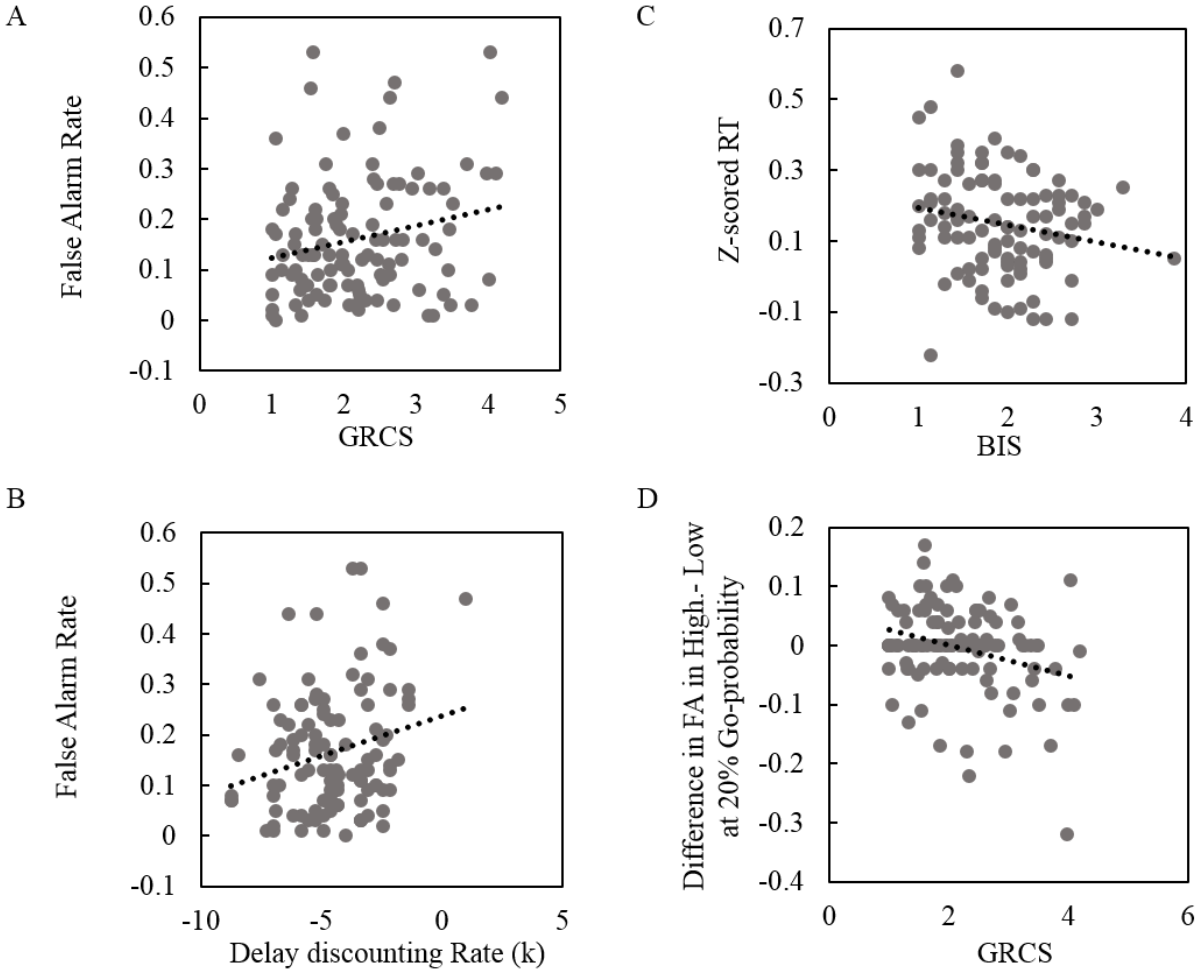


Figure 4: The correlations between the performance of Speed-Rewarded Go-NoGo task and the impulsive and risk-taking tendencies. (A) The correlation between GRCS total score and false alarm rate; (B) the correlation between delay discounting and false alarm rate; (C) the correlation between BIS score and Z-scored RT; (D) the correlation between the GRCS total score and the difference of false alarm rate between high and low reward conditions.

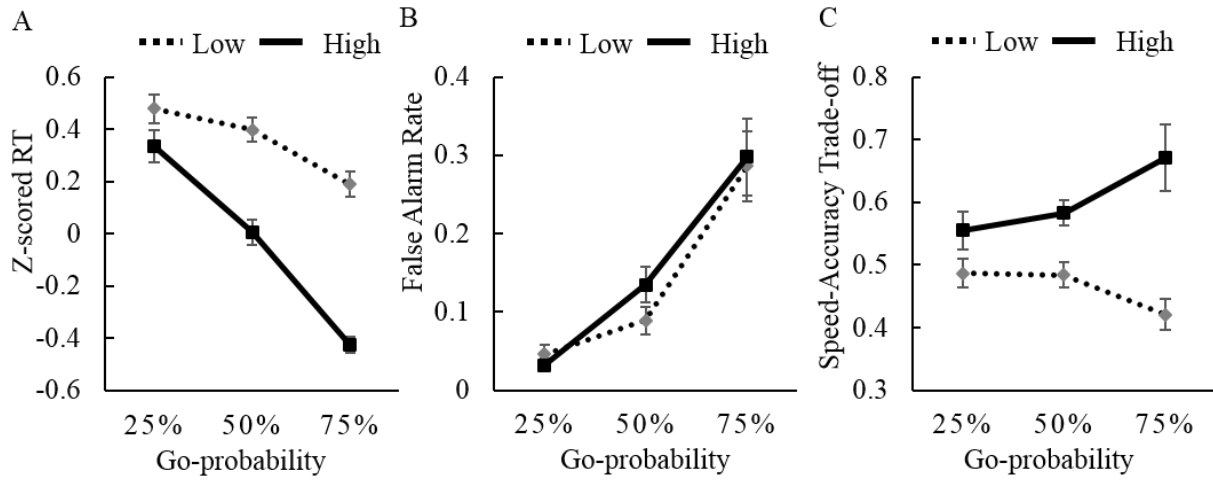


Figure 5: Performance of Speed-Rewarded Go-NoGo task (study 2). (A) The Z-scored RT, (B) false alarm rate, (C) Speed-accuracy trade-off.

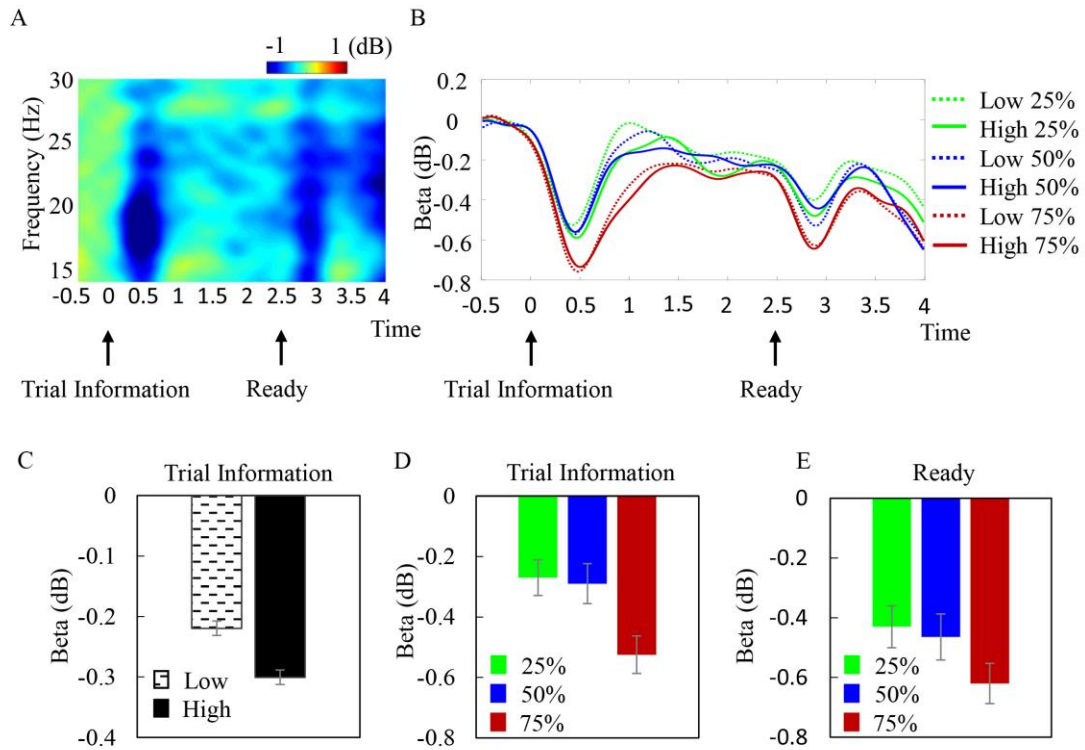


Figure 6: EEG beta band activity in left sensorimotor region during Trial Information and Ready period. (A) Time-frequency map of the beta band power across all the trials. (B) The mean beta band power in each Reward and Go-probability condition. (C) Left: the main effect of Reward during Trial Information period; Middle: the main effect of Go-probability during Trial Information period; Right: the main effect of Go-probability during Ready period.

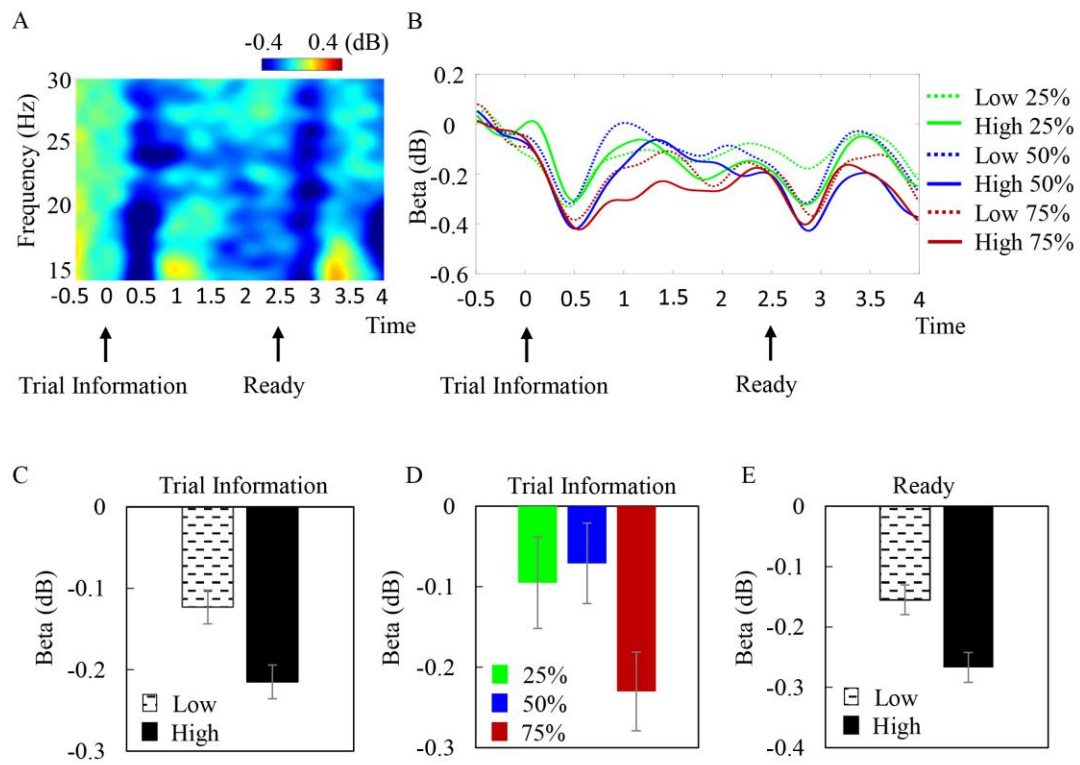


Figure 7: EEG beta band activity in right prefrontal region during Trial Information and Ready period. (A) Time-frequency map of the beta band power across all the trials. (B) The mean beta band power in each Reward and Go-probability condition. (C) Left: the main effect of Reward during Trial Information period; Middle: the main effect of Go-probability during Trial Information period; Right: the main effect of Reward during Ready period.

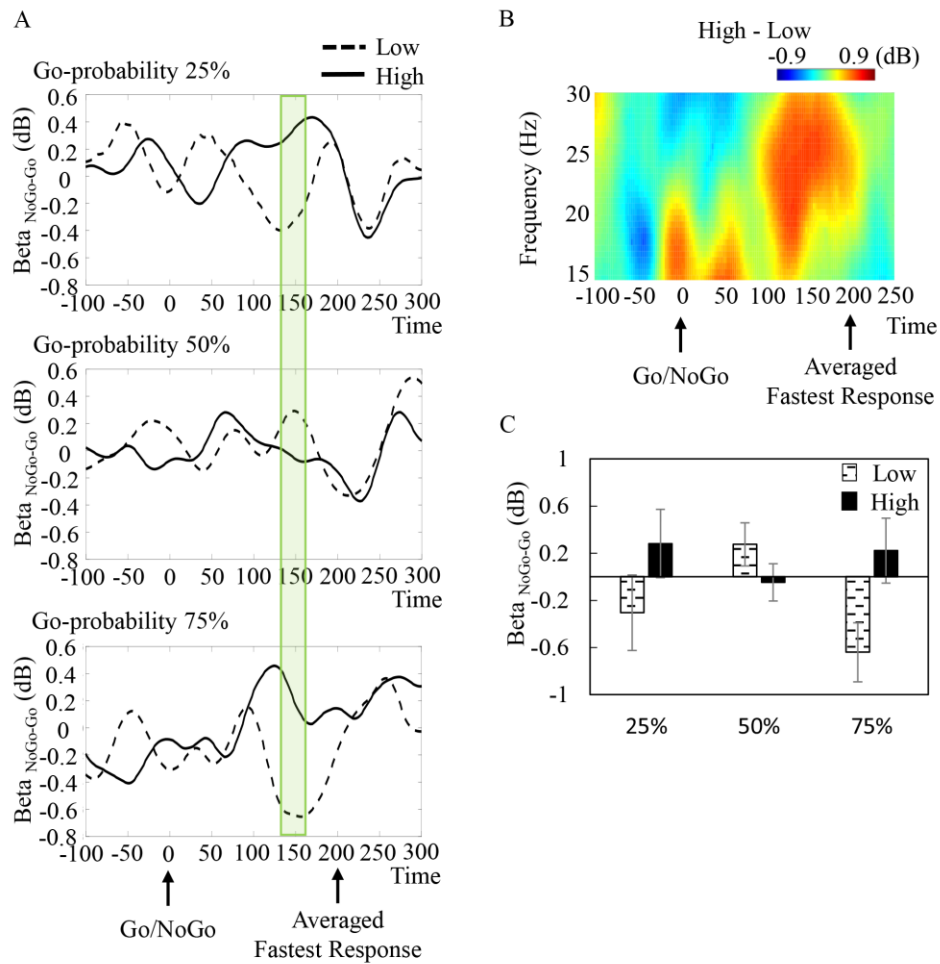


Figure 8: EEG beta band activity in right prefrontal region during Go/NoGo period. (A) The mean of the beta power_{NoGo – Go} during Go/NoGo period under each Reward and Go-probability condition. (B) Time-frequency map of the difference in beta power_{NoGo – Go} across high and low reward conditions (High-Low). (C) The interaction between Reward and Go-probability on beta power_{NoGo – Go} during the GO/NoGo period.

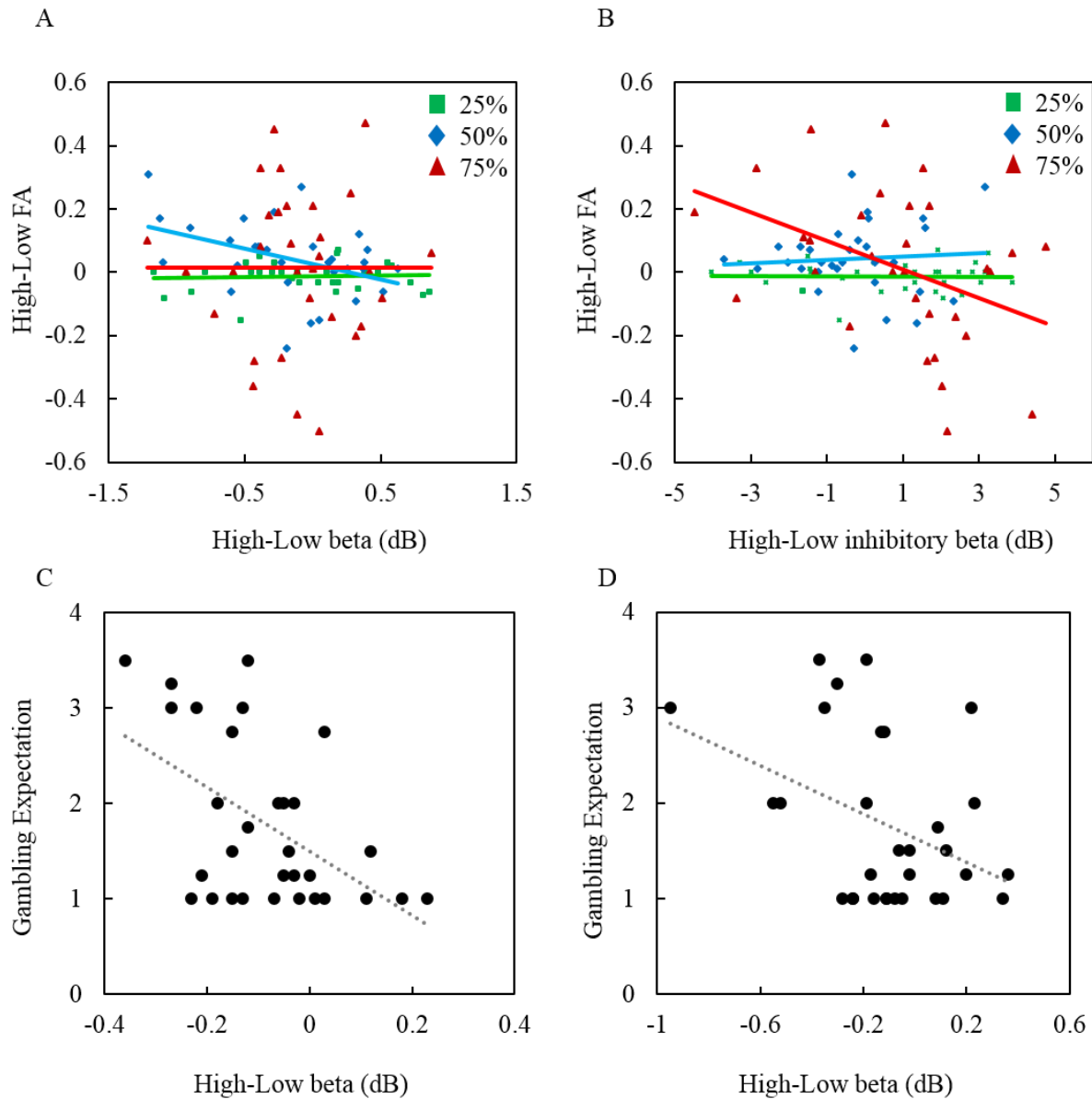


Figure 9: Beta oscillations can predict the performance of Speed-Rewarded Go-NoGo task and the personal trait related with risk taking and impulsive tendencies. (A) Beta oscillation during Ready period from right prefrontal region can predict the FA in Speed-Rewarded Go/NoGo Task. (B) Beta oscillation during Go/NoGo Period from right prefrontal region can predict the FA in Speed-Rewarded Go/NoGo Task. (C) Beta oscillation during Trial Information period from left sensorimotor cortex can predict the Gambling Expectation score. (D) Beta oscillation during Ready period from right prefrontal region can predict the Gambling Expectation score.

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