平成　27 年度　学位論文（博士）要旨

玉川大学大学院脳情報研究科

論文題目	Reward-Predictive Stimuli Enhance Post-Error Uncertainty in the Cingulate Cortex
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論文要旨

Imagine the chaos of a world where nobody ever admitted to or learned from their mistakes. Even when nobody explicitly tells us that we are wrong it is often important for us to be cognizant of potential errors in our decisions. Consequently we must continue to monitor how likely our decisions seem to have been erroneous even after we have committed to them. Many studies have provided behavioral and neural evidence that we do just this (e.g. Carter et al., 1998; Carter, MacDonald, Ross, & Stenger, 2001; Garavan, Ross, Kaufman, & Stein, 2002; Kerns et al., 2004; Kiehl, Liddle, & Hopfinger, 2000; Menon, Adleman, White, Glover, & Reiss, 2001; Rabbitt, 2002, Rabbitt & Vyas, 1981).

Interestingly, the neural regions related to the monitoring of error after decision, such as the cingulate and insular cortices, are densely connected with the classic reward processing system (Berger, Gaspar, & Verney, 1991; Gaspar, Berger, Febvret, Vigny, & Henry, 1989; Williams & Goldman-Rakic, 1993). Therefore, these regions are ideally positioned to be able to combine the processing of error and the processing of reward value. A few studies have investigated the potential influence of reward value on error-monitoring. In these studies subjects were rewarded for correct but not incorrect responses and therefore the effects of accuracy and reward were confounded. Consequently whether or not error-processing differs when responses are made to stimuli associated with different reward values remained yet to be determined. However, the reward value associated with stimuli has been shown to increase their processing prior to decision responses (e.g. Theeuwes & Belopolsky, 2012). We therefore hypothesized that if there are similar effects on information processing subsequent to decision responses, then because error-monitoring depends on continued processing of information after decisions, the reward value associated with stimuli might impact upon the processing of error.

We set out to examine this hypothesis using a perceptual decision making task. In each trial of our experiments participants saw a cloud of small white dots, of which a certain percent moved coherently to the left or the right, and of which the rest moved randomly. In some trials more dots moved coherently meaning that the global motion direction should have been easier to perceive and in other trials less dots moved coherently meaning that the global motion direction should have been more difficult to perceive. Participants' task was to indicate whether they perceived leftwards or rightwards global motion of the dots. Subsequently they were provided with a rewarding or a non-rewarding outcome. Importantly, unlike previous studies, this outcome was not contingent on participants' response accuracy but rather on the dot motion direction of stimuli (these associations were counterbalanced between participants). Therefore, if the dots moved in the direction associated with reward (e.g. left) then participants received the rewarding outcome regardless of whether they correctly picked this direction or incorrectly picked the other direction. Likewise, if the dots moved in the direction associated with non-reward (e.g. right) then participants received the non-rewarding outcome regardless of whether they correctly picked this direction or incorrectly picked the other direction. This allowed us to test, under both easier and more difficult conditions of stimulus perceivablity, correct and error trials in which stimuli were completely reward predictive and correct and error trials in which stimuli were completely non-reward predictive.

Behaviorally we found that participants were faster to respond in correct trials, and particularly so in the easy perceivability condition. Importantly, within correct trials in this condition, participants responded significantly faster to stimuli that were predictive of reward than to stimuli that were predictive of non-reward. Using functional magnetic resonance imaging (fMRI), we examined neural activity in the rewarded correct, rewarded error, non-rewarded correct, and non-rewarded error conditions. Our main finding supported our hypothesis by showing an error-processing by reward value interaction in the midcingulate cortex (MCC) that occurred at a response time; i.e. when participants had committed to a decision but not yet received feedback about its accuracy. Activity here significantly discriminated between erroneous and correct decisions in trials in which stimuli were predictive of reward compared to those in which stimuli were predictive of non-reward.

In a second experiment, we got participants to do a similar task that had two differences to the task used in experiment one: (1) they received a secondary reward (money) rather than the primary reward that was used in experiment one (juice), and (2) they rated how confident they felt that they had made the correct motion-discrimination response before receiving the outcome. In this experiment the response time results of experiment one were replicated, and confidence ratings were found to follow a similar pattern to these. Specifically confidence ratings were higher in correct trials and especially so in the easier condition. Importantly, within correct trials in the easy perceivability condition, participants responded with significantly more decision confidence to stimuli that were predictive of reward than to stimuli that were predictive of non-reward. Therefore, the behavioral results of both experiments showed that when stimuli can be easily perceived, the reward value associated them impacts on behavior by decreasing the speed of correct responses and increasing self-reported confidence to them.

Using ROIs defined around the peak coordinates of the interaction we found in the MCC in experiment one, we were able to replicate this interaction in experiment two. Considering that the reward, the participants, and the some aspects of the task, were different to experiment one, this shows that this is a robust effect. In particular, because previous studies have shown differential neuronal activations for primary and secondary rewards (e.g. see Sescousse, Caldu, Segura, & Dreher, 2013) this result shows that this effect is more generalizable than might be expected.

Importantly, we found that activity in the exact same regions of the MCC correlated negatively with participants’ self-reported levels of confidence. This correlation was significant even when only easily perceiveable correct trials were included in analysis, indicating that this isn’t an effect specific to error trials or to trials with low perceivability. Instead this result indicates that the activity in the MCC that we found to be affected by the reward value of stimuli likely reflects decision uncertainty, which is defined as being the perceived likelihood of being incorrect (e.g. see the model of Kepecs, Uchida, Zariwala, & Mainen, 2008, or alternatively the brief explanation of this in Appendix B). This therefore has implications for theories of decision uncertainty and confidence (defined in the same model as the inverse of uncertainty).

The design of our task meant that while participants' response would not affect which outcome they received, when they did receive outcome participants could thereby infer the direction that dots must have moved in and therefore whether or not their response had been correct (e.g. "I received reward so the dots must have moved left, but I responded that they moved right, so I made an error"). We found that error was processed in non-reward conditions but not in reward conditions at this time.

One potential explanation of our task, that fits with "evidence accumulation" models of error-processing and uncertainty (see Yeung & Summerfield or Appendix A for a summary), but remains to be formally tested, is that the reward value associated with stimuli affected how much these continued to be processed after a decision had been made. In trials with reward predictive stimuli, the finding that uncertainty processing in error trials occurred after committing to a decision but prior to receiving feedback might indicate that these stimuli continued to be processed after a decision to them was made. On the contrary, the finding that error processing did not occur prior to feedback in trials with non-reward predictive stimuli may indicate that these were processed to a lesser degree after a decision was made.

Overall, the results of the current study extend previous knowledge about error-processing and uncertainty by showing that these are influenced by the reward value of stimuli even when response accuracy and the reward value of outcome are dissociated. This has various implications for current models of error-processing, confidence/uncertainty, and cingulate cortex function, and these are discussed in detail in the general discussion of this thesis.

平成２７年度　学位論文（博士）審査票

玉川大学大学院　脳情報研究科											専攻　博士課程後期
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論文題目	Reward-Predictive Stimuli Enhance Post-Error Uncertainty in the Cingulate Cortex										
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審査要旨

報酬／無報酬と成功／失敗とは通常はリンクされている。学位申請者による本研究は、これらの要因を分離し、両者の相互作用と意思決定における不確実性との関連を調べたものである。

報酬／無報酬とランダムドットモーションの向き（右／左）との連合学習課題を行っている被験者の脳活動を、刺激のコヒーレンシーの操作により正答率を調整しつつ計測することによって、両者の脳内情報処理が帯状回の部位毎に分離して処理されていること、行動選択時に報酬／無報酬と成功／失敗の情報が相互作用する脳領域が帯状回中部であることを見出すとともに、同部位における失敗関連の脳内情報処理が confidence の低さに基づく saliency によって亢進することを示した。これらの所見は、従来から指摘されている帯状回の機能である「失敗尤度表現」が、失敗後の行動調整に関わるメカニズムの一端を明らかにするものであり、この研究分野の進展の重要な一歩である。

認知制御の起始部位としての帯状回の機能の本質は、認知神経科学の一大トピックであり、帯状回機能を統一的に説明する認知神経科学的仮説が最近注目されている。この問題に新たな視角からアプローチした点で、学術的な意義の高い研究であり、本研究の一部は日本神経科学学会の学会誌である Neuroscience Research 誌に受理済みである。さらに、学術論文としては未発表であるとは言え、発表済みの所見を補強する重要な所見を既に得ており、さらなる発展も期待できる。以上のことから、博士（学術）の学位を授与するための要件を十分に満たしていると判断する。

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