PERCEPTUAL TUNING AND FEEDBACK-RELATED BRAIN ACTIVITY IN GAMBLING TASKS

by

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To my family

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Chapter I Introduction

1. Background knowledge about the event-related potential technique

1.1 A bit of history

When two electrodes are placed on the human scalp, a pattern of variation in voltage over time will be revealed through an appropriate amplifier. This electrical activity of the brain, called electroencephalography (EEG), results from ionic currents generated by biochemical processes at the cellular level. The scalp EEG specifically measures summated activity of post-synaptic currents; its amplitude varies between approximately -100 and +100 μV and its frequency ranges to 40 Hz or more (Coles & Rugg, 1995). In 1929, Hans Berger published the first report on human EEG (Berger, 1929).

In the following decades, EEG has been proved to be very useful in both scientific research and clinical applications. However, EEG, in its raw form, reflects thousands of simultaneous ongoing brain processes, making it difficult to isolate the brain responses to a certain stimulus or event of interest. It is possible to extract the neural responses specific to researchers' interest from the overall EEG, and get a set of voltage changes within an epoch of EEG that is time-locked to some event, which is called the event-related potential (ERP).The most commonly used signal extraction technique is averaging, in which the digital EEG voltage values for each time-point in the epoch were averaged to yield a single vector of values representing the average activity at each time point, as shown in the grand average waveforms of the most ERP research publications. The ERP amplitude, on the order of microvolts, is much smaller than the EEG amplitude. The first unambiguous sensory ERP recordings from awake human were published in 1939 (Davis et al., 1939; Davis, 1939)

The computer revolution of the 1940s brought profound influences to the ERP research field. In one aspect, the computer revolution led to a ‘cognitive revolution’ in psychology during the 1950s and 1960s, with the focus upon internal mental processes in the information processing framework as opposed to the focus on overt behavior proposed by behaviorism. As cognitive processes are implemented by the brain, it is quickly recognized that ERPs or measures of brain activity might index or provide insights into psychological processes. In another aspect, the computer revolution allowed the EEG signals to be recorded and analyzed with great efficiency. Furthermore the advanced sampling and amplifying technique and hardware enabled high quality EEG signals recordings with lower noise levels. Galambos and Sheatz published the first computer-averaged ERP waveforms in 1962 (Galamobos & Sheatz, 1962).

1.2 Advantages and disadvantages of the ERP technique

Comparing to reaction time, the ERP technique is appealing because it can provide on-line measurement of cognitive processing. It records brain activity at a temporal resolution on the order of milliseconds, allowing measurements as the process of interest unfolds so that stage of processes could be monitored. In addition, ERPs are multidimensional (varying in polarity, latency, amplitude and scalp distribution), and can be recorded without explicit behavioral responses. The functional significance of the ERP results, however, is not always as clear as that of a behavioral response. Researchers should be very cautious when they make psychological inference when they use the ERP technique (see Rugg and Coles, 1995). Furthermore, the small amplitude of the ERPs requires a larger number of trials in order to measure them accurately. Thus the ERP method is not good for studies in which large number of trials could not be implemented either because of the task characteristics or the participant populations.

The advent of positron emission tomography (PET) in the 1980s, and subsequently functional magnetic resonance imaging (fMRI) in the 1990s triggered an explosion of interest in relating cognitive function to human brain activity. While these hemodynamic measures have a spatial resolution in the millimeter range, the spatial detail of conventional ERP recordings has been coarse and hard to define, because of the inverse problem (i.e., the estimation of intracerebral sources responsible for a given scalp potential has no unique solution.) and skull conductor effect (the distortion of neuronal potentials as they are passively conducted through the highly resistive skull). To some extent, the popularity of these new neuroimaging tools moved researchers' interest away from electroencephalography for research and clinic uses. Nevertheless, ERPs have a temporal resolution of 1 ms or better, which hemodynamic measures cannot match due to the sluggish nature of the hemodynamic responses.

In summary, the ERP technique has its own significant advantages and disadvantages compared to reaction times and hemodynamic measures. Some research questions are suited for using the ERP technique, others are not. For example, if someone is interested in the brain localization of a given cognitive function, the ERP measurement would not be recommended. However, "knowing where" is not equal to "knowing how." ERPs can be very useful in elucidating cognitive mechanisms and their neural substrates even when there is no knowledge about the neural generation (Luck, 2006).

1.3 ERPology and ERP components

There are two lines of ERP research. One line of research has been focused on discovering and understanding ERP components (e.g., the contingent negative variation or CNV, the P300 and the N2); the other line of research is to use those identified ERP components to address scientific questions. The former line of research is called the ERPology (Luck, 2006). The popularity of ERPology in the 1970-80s resulted in a better refinement and understanding of the ERP components. It is apparent that the other line of the ERP research has to be built on ERPology, since it is necessary to know the characteristics of a specific ERP component before one can use it as an index (like the role of reaction time in cognitive psychology) to study research questions in psychology and related fields. On the other hand, the focus upon the study of specific components made ERP research not very interesting, popular and easy to use among cognitive psychologist and neurologist. In the recent three decades, more and more ERP research has been devoted to elucidating the cognitive processes that underlie observed behaviors, and ERP methods have prospered in today's psychological research.

ERP components are manifestations of the brain activities invoked by the underlying mental activity. An ERP component could be defined by a combination of its polarity (i.e., a positive peak or negative trough), its characteristic latency (i.e., the temporal relationship between the feature of the waveform and the stimulus or event of interest), its distribution across the scalp (i.e., relative amplitude at different recording sites on the scalp), and its sensitivity to characteristic experimental manipulations (e.g., early attention selection or memory process). There are two general classes of ERP components (Hillyard & Kutas, 1983): *exogenous components*, which occur within around 100 ms after stimulus onset, and are believed to reflect the peripheral sensory processing to physical parameters of the stimulus; and *endogenous components*, which occur 100 ms or more after stimulus onset, and are believed to reflect the cognitive process of perception, attention, memory, decision, response preparation, and so on. Cognitive psychologists are mostly concerned with the endogenous components.

The first cognitive ERP component to be discovered was the Contingent Negative Variation or CNV, reported by Grey Walter and his colleagues (Walter et al., 1964). Their paradigm consisted of the presentation of pairs of stimuli (e.g., a click warning signal followed by a flickering light target), separated by a time interval (e.g., 1 second), and the establishment of a contingency between the stimuli (e.g., press a button upon detecting the flickering light which followed the click). In their study, during the interval between the warning signal and the target stimulus, a large negative voltage was observed at frontal electrode sites. This negative voltage is the CNV, which has a ramp-like shape and tends to reach its maximum at around the time of the target onset. It was originally suggested to reflect the subject's preparation for the upcoming target. Inspired by the finding of this first cognitive ERP component, more and more researchers have devoted themselves to ERP research, leading to the discovery of more cognitive ERP components. Some of them are introduced in the following section as they are related to this dissertation research.

2. Relevant ERP components

2.1 The P300

As the most studied ERP component, the P300 component is usually identified as a parieto-central positive voltage deflection in the ERP waveform that varies with the probability of the eliciting stimulus or event (Fabiani et al., 1987; Picton, 1992). It was first reported by Sutton and his colleagues (Sutton et al., 1965). In their experiment, they presented a series of pairs of stimuli (a cueing stimulus and a test stimulus), and participants were instructed to respond to the test stimulus. For some pairs the cueing stimulus was always followed by the same test stimulus; for others the cueing stimulus could be followed by two different test stimuli. On the trials participants could not predict their response according to cueing stimulus, a large positive voltage deflection was elicited, and peaked around 300 ms after stimulus onset, based on which the P300 component got its name. However, the peak latency of the P300 component may range widely, from 250 ms and extending to 900 ms, depending on various experimental manipulations. The P300 has also been called the P3 wave, because it is the third major positive peak in the late sensory potential (Ritter et al., 1968).

In subsequent research, the standard paradigm adopted to elicit the P300 is the “oddball” task, in which a series of events, which comprise a frequent type and a rare type, are presented, and participants are required to in some way respond to the rarer of the two event types. At least two ERP components, called P3a and P3b, have been identified in the time range of the P3 wave. The P300 or P3 found by most ERP researchers in the classical oddball task actually refers to the P3b component. In other studies, where a third event is introduced into the oddball task, e.g., a ‘dog bark’ in the context of high and low tones, the novel stimuli elicited a positive voltage deflection as large as the P3b, but with an earlier peak latency and a more frontally-oriented topography (Courchesne et al, 1984; Knight, 1984). This early positive component has been referred to the P3a (Coursechene et al., 1975; Squire,

Squire, & Hillyard, 1975), or labeled as the frontal P3, and has been linked to processes involved in the involuntary capture of attention by a salient event (Knight, 1991).

The usual interpretation of P300 latency is that it is a metric of stimulus evaluation time (Kutas et al., 1977; Magliero et al., 1984), and is unrelated to response selection and execution processes (Duncan-Johnson, 1981; McCarthy & Donchin, 1981; Ritter et al., 1983, but see Pfefferbaum et al., 1986; Ragot, 1984). For example, the P300 latency varied with the ease of categorizing events in one class or the other—the more difficult the categorization processes, the longer the P300 latency. In normal subjects, P300 latency is correlated negatively with cognitive performance (Polich et al., 1983; Johnson et al., 1985). In patients with decreased cognitive ability, the P300 is later than in age-matched normal subjects (Brown et al., 1982; Homberg et al., 1986; O'Donnell et al., 1987).

The hallmark of the P300 amplitude is that it was inversely proportional to the target probability, which has been observed in every type of task from simple counting (Duncan-Johnson & Donchin, 1977; Johnson & Donchin, 1980, 1982; Kutas, McCarthy, & Donchin, 1977; Picton & Hillyard, 1974) and reaction time paradigms (Duncan-Johnson & Donchin, 1982; Kutas et al., 1977), to prediction (Friedman et al., 1973; Tueting, Sutton, &Zubin, 1970) and feedback tasks (Campbell et al., 1979). When the probability of the task-defined stimulus class gets smaller, the P300 amplitude gets larger. Moreover the P300 amplitude varied with the sequential expectancies subjects developed during the experiment. Repetitive stimuli elicited a smaller P300 than non-repeated stimuli (Squires et al., 1976; Duncan-Johnson & Donchin, 1977; Johnson & Donchin, 1980, 1982; Tueting et al., 1970). In addition, P300 amplitude is sensitive to the amount of attentional resources engaged during dual-task performance. As the primary cognitive task is more difficult and demands a lot of cognitive resources, P300 amplitude from the secondary oddball task decreases (Isreal et al., 1980; Kramer et al., 1985). Furthermore, when the task of discriminating the target stimulus from the standard stimulus is too difficult, participants become uncertain of whether a given stimulus is a target or non-target, and the amplitude of the P300 wave becomes smaller.

Johnson (1984, 1986) proposed a *triarchic* model to explain the P300 amplitude changes induced by various experimental manipulations: P300 amplitude = f [T × (1/P + M)], where P denotes subjective probability, M denotes stimulus meaning and T denotes amount of information transmitted. Subjective probability appears to combine both global and local expectancies (Picton, 1992). Stimulus meaning is composed of three dimensions: task complexity (the extent to which a stimulus must be processed), stimulus complexity (perceptual demand to discriminate the stimulus features), and stimulus value (significance of the event to be detected). Amount of information transmitted depends on equivocation in the stimulus evaluation and attention paid to the task. In this model, the subjective probability and the stimulus meaning are independent of one other; both are modulated by a third factor that represents the proportion of the stimulus information received. The P300 process may not be unitary but represents the sum of several different cognitive processes.

In addition, P300 amplitude and latency are correlated negatively (Polich, 1986, 1992). This is partly due to the issue of "the latency jitter" (i.e., variation in single trial latencies reduce the amplitude of an ERP component when using the signal averaging method), and could also result from other cognitive processes related to the task that precede P300 generation. Several studies have shown that the latency and the amplitude of the P300 may be differentially affected by experimental variables (Picton et al., 1978; Johnson, 1986; Kutas et al., 1977). Therefore researchers should be cautious in interpreting the amplitude and latency of the P300 in any experiment in which a large amount of latency variability is expected (Johnson, 1986).

A major theoretical interpretation of the P3 wave is that it is related to "context updating" (updating one's representation of the current experiment) in working memory (Donchin, 1981; Donchin & Coles, 1988). It has been suggested that after initial sensory processing, an attention-driven comparison process evaluates the representation of the previous event in working memory (Heslenfeld, 2003; Kujala & Naatanen, 2003). An update is necessary when a new stimulus is detected. The P300 may represent the control of this updating process (Metcalfe, 1992). The most direct supporting evidence for this theory has come from the observation that larger P300 amplitudes are associated with superior memory performance (e.g., Fabiani et al., 1990; Noldy et al., 1990). However, not all studies have observed this effect (see Verleger, 1988 review). While the context updating theory remains popular in the P300 research field, some new theories with different emphases have emerged as well (e.g., Nieuwenhuis et al., 2005a; Verleger et al., 2005).

With more and more knowledge gained from the thousands of published P3 experiments, the ERPology of the P3 research has been beneficial to the development of several other disciplines. For example, it has been widely used as a dependent index in studies of cognitive aging (e.g., Fjell & Walhovd, 2001), pharmacological research (e.g., Sanz et al., 2001), studies of clinical disorders (e.g., Mathalon et al.,2001; Polich et al., 1986) and even criminal psychology (e.g., Kiehl et al., 1999); the P300 latency has been used to demonstrate the cognitive dysfunction occuring in early dementia or in metabolic disorders (in Polich review, 1995); and the P300 amplitude has been used with the guilty knowledge techinque to investigate crimes and exonerate innocent suspects (Farwell & Donchin, 1991; Farwell & Richardson, 1993; Farwell & Smith, 2001).

2.2 The N2 family

2.2.1 Early classifications

The N2 is a negative voltage deflection peaking between 200 and 350 ms following the presentation of a specific visual or auditory stimulus. The label ‘N2’ reveals that it is the second major negative peak in the ERP average waveform. It is often observed in combination with the P300 but with smaller amplitude and earlier latency. In early research, the N2, together with the P300, was sometimes referred to as the ‘N2-P3’ complex (Squires et al., 1977; Squires et al., 1976). As with the P300, the initial paradigm to study the N2 component is the oddball task in which the presentation of the rarer event elicits the N2.

Several distinct N2 potentials have been characterized (reviewed by Pritchard et al., 1991). The mismatch negativity (the MMN, sometime referred to as the N2a), a difference wave obtained by subtracting the ERP wave for the frequent standard event from the ERP wave for the rarer deviant signal, peaks at around 200 ms with an anterior cortical distribution and is typically found in auditory oddball paradigms (for MMN reviews, see Näätänen, 2001; Näätänen & Alho, 1997; Ritter et al., 1995). Visual mismatches do not seem to elicit exactly the same sort of the N2a, so the MMN is modality-specific. MMN is present even when the auditory stimuli are unattended or task-irrelevant. Furthermore, the MMN amplitude was illustrated to be sensitive to the degree of physical deviance of the current stimulus from the prevailing context. Therefore Näätänen and his colleagues suggested that the MMN likely represents an automatic novelty-detection process (Näätänen et al., 1978).

A second N2 component (N2b) peaks a little later and its presence depends on the event being attended. N2b is larger for rarer events than for frequent events (Ritter et al., 1982; Ritter et al., 1983; Simson et al., 1977). It has also been shown to be larger in response to nontargets than in response to targets (Näätänen et al., 1982; Sam et al., 1983). N2b is largely centered on the vertex (Cz) with some variation along the anterior-posterior axis in different experiments in both auditory and visual modalites (in Pritchard et al., 1991 review).

Sometimes another N2 component, called the N2c, was categorized as reflecting the conscious perception of the stimuli as well; however, it was larger for targets than for non-targets in categorization tasks (reviewed by Pritchard et al., 1991), and its scalp distribution was modality specific, being more lateral and posterior in the visual modality and frontal/fronto-central in the auditory modality.

2.2.2 Recent developments

In the last two decades, special attention has been given to an anterior N2 component, referred to as the negative-going wave with a frontal or central scalp distribution, and mostly corresponding to the N2b in Pritchard et al.'s (1991) classification. Folstein and van Petten (2008) have recently given a thorough review on this topic. In their review, two types of anterior N2 have been discussed: one is the *anterior mismatch N2*, which likely reflects the attended mismatch between a stimulus and a mental template; the other is the *cognitive control N2*, which may be related to mental processes related to response inhibition, conflict detection, error detection, or strategic performance monitoring.

2.2.2.1 Anterior mismatch N2

The most straightforward task to demonstrate an anterior mismatch N2 is the sequential matching task, in which subjects are asked to judge whether a second stimulus is the same or different from an initial stimulus. When the second stimulus does not match the first one, the anterior N2 elicited by the second stimulus is larger compared to when the second stimulus matched the first one (Wang et al., 2003; Cui et al., 2000; Kong et al., 2000). Furthemore, Wang and colleagues (2004) found that partial mismatch yielded an N2 that is intermediate between complete matches and complete mismatches, as expected from a template-matching process. This N2 effect is eliminated when mismatch is task irrelevant (Fu, Fan & Chen, 2003).

In addition, the anterior mismatch N2 has been observed in revised versions of the oddball paradigm. For example, Breton and colleagues (Breton et al.,1988) recorded a larger anterior N2 to the rare letter as compared to the frequent stimulus when participants were asked to make RT responses to the rare letter. Furthermore, this anterior N2 effect was larger when the rare target could be any other letter of the alphabet except the frequent standard letter (e.g., X), compared to when the rare target was always a specific letter (e.g., O). In either condition, the standard/rarer rate for the oddball task was 80/20. Furthermore, complex rare novel stimuli elicited a larger anterior N2 than simple rare novel stimuli when both were equally rare (Courchesne et al., 1975; Czigler & Balazz, 2005; Daffner et al., 2000). Compared to the simple novel stimuli, complex novel stimuli are meaningless, and are more deviant from long-term memory representations. Therefore the N2 novelty effect elicited by the complex novel stimuli was larger at the beginning of experiments (Daffner et al., 2000; Folstein & van Pettern, 2008). However, it decreased rapidly with habituation when stimuli were repeated (Courchesne et al., 1975).

Overall, the experimental results reviewed above are consistent with the claim that the anterior N2 is sensitive to the perceptual mismatch between the current stimuli and a mental template. This mental template could be formed by both long-term memory and the short-term task situation (see in Folstein & van Pettern, 2008 review).

2.2.2.2 Cognitive control N2

Cognitive control is used to describe a variety of cognitive processes (e.g., response inhibition, conflict detection or strategic performance monitoring) that the brain uses to guide thought and behavior. In the following sections, several cognitive tasks commonly used in the study of these cognitive control processes, as well as the N2-like ERP components evoked in these task, are reviewed, including No-go N2 in the Go/No-go task, conflict N2 in the flanker task and error-related negativity in general speeded reaction time tasks.

2.2.2.2.1 The No-go N2 in Go/No-go task

The Go/No-go task is frequently used in cognitive psychology and cognitive neuroscience research to evaluate the processes and mechanisms related to response inhibition. Its history can be traced back to Donders (1868/1969). The classic task usually involves only two stimuli: a Go stimulus and a No-go stimulus. Subjects are required to make a quick response to the Go stimulus but withhold their response to the No-go stimuli. Typically Go stimulus is set to be more frequent in order to build up a prepotent tendency to respond, therefore increasing the inhibitory effort necessary to successfully withhold response to No-go stimuli. A larger anterior N2 is elicited by No-go than by Go stimuli. This No-go N2 is sensitive to speed pressure, the amplitude being larger when subjects were required to respond quickly (Jodo & Kayama, 1992). The No-go N2 is also larger in participants with lower false alarm rates, suggesting its association with successful response inhibition (Falkenstein, Hoorman,& Hohnsbein, 1999). Furthermore, a larger N2 was observed for No-go stimuli that look more like the Go stimulus (Azizian et al., 2006), probably because the shared features between No-go and Go stimuli increased the tendency to respond in No-go trials, requiring greater effort for inhibition. These studies provided strong support that the observed No-go N2 indexes cognitive control rather than perceptual mismatch.

2.2.2.2.2 The conflict N2 in Eriksen flanker tasks

The Eriksen flanker task (Eriksen & Eriksen, 1974) is another task which is often used in cognitive control research. In the classical Eriksen flanker letter task, subjects carry out a speeded response to a target letter which is closely surrounded by non-target letter or flankers. Typically two conditions are involved in this task: a congruent condition, in which the central letter is surrounded by four identical flanker letters (e.g., HHHHH), and an incongruent condition, in which the central letter is surrounded by four flanker letters indicating the opposite response (e.g., SSHSS). Reaction time is invariably found to increase in the incongruent condition compared to the congruent condition. In addition, an enhanced frontocentral N2, together with a delayed parietal P3, have been observed in the incongruent condition compared to the congruent condition (Gehring et al., 1992; Kopp et al., 1996).

This anterior N2 is largest for highly probable stimuli (Bartholow et al., 2005), which makes it difficult to account for within a mismatch-based theory. Furthermore, this N2 appears to be sensitive to response conflict but not stimulus conflict: stimuli that present incongruent information but require the same responses do not enhance the N2 (van Veen & Carter, 2002). A recent conflict monitoring theory (Yeung, Cohen, & Botvinick, 2004) proposed that the N2 elicited in the flanker task reflected the detection of response conflict in correct trials *before* the response; in contrast the error-related negativity (the ERN, see below) reflected the detection of a response conflict in the error trials *after* the response.

2.3 The error-related negativity

The error-related negativity (ERN or Ne) is a negative voltage deflection peaking within 100 milliseconds (ms) of error commission, observed in speeded choice reaction time tasks (Falkenstein et al., 1990, 1991; Gehring et al., 1990, 1993). Different from the other ERP components, the ERN waveform is response-locked rather than stimulus locked, that is, the epoch used for signal averaging was extracted based on the temporal location when a response occurred, and the time zero in the waveform indicated an erroneous response execution rather than the onset of a stimulus presentation (as in the stimulus-locked waveform). Studies have shown that the ERN has a frontocentral scalp distribution, and dipole modeling and fMRI evidence points to a likely generator in the anterior cingulate cortex (ACC) or adjacent supplementary motor area (Dehaene et al. 1994; Kiehl et al., 2000; van Veen & Carter, 2002; Hermann et al., 2004). The ERN amplitude is larger when accuracy is emphasized by instruction, than when speed is emphasized (Gehring et al., 1990, 1993; Falkenstein et al., 1990, 2000). Together with the findings that the ERN is larger when correct trials have high monetary value or when subjects believe that their performance is being evaluated by others (Hajcak et al., 2005b), this suggests that ERN is sensitive to the motivational significance of the errors (Gehring et al., 1993).

2.3.1 Error-detection theory

The response-locked ERN was originally interpreted as a correlate of error detection on the basis of response representations (Falkenstein et al., 1991; Gehring, 1993). Specifically, in speeded-response tasks, the neural representation of an erroneous pre-mature response was compared with the representation of the correct response which is derived from the continuous stimulus processing even after response execution. A discrepancy between these two representations gives rise to a mismatch or error signal, which is manifested in the ERN. This error detection hypothesis was directly supported by the finding that the ERN is smaller on errors in which the mismatch between required and executed response is smaller (e.g. finger errors versus hand errors) (Falkenstein et al, 2000; Bernstein, Coles, & Schefferes, 1995, but see Gehring & Fencsik, 2001). The finding that the ERN occurs even after partial errors when the exerted force is not sufficient to produce overt errors (Scheffers et al., 1996), together with the finding that ERN-like negativity was also elicited on the correct response in some studies (Vidal et al., 2000), suggest that the ERN could reflect the operation of the comparison process itself (Falkenstein et al., 2000).

2.3.2 Conflict monitoring theory

The conflict-monitoring theory was proposed as an alternative to the error-detection theory (Carter et al., 1998; Botvinick et al., 2001). It asserts that the ERN reflects the detection of larger response conflict on error trials than on correct trials after response execution. In order to generate a conflict signal, the monitor or comparator does not need to know which response is correct. Instead, the error could be detected through detecting two competing responses which are simultaneously active. The computational model of the conflict monitoring theory has mimicked the time-course of the ERN and its sensitivity to a variety of experimental manipulations (Yeung et al., 2004). For example, a change in attentional focus and an application of a stricter response criterion can produce effects similar to accuracy emphasis on the ERN. However, it is hard for the current conflict monitoring model to explain the response-locked ERN activity on correct trials, since according to their computational model, conflict-related activity on correct trials should be observed before the response as manifested by the stimulus-locked anterior conflict N2 in high conflict trials (Yeung et al., 2004)), but not after the response in the latency range of the ERN.

3. Feedback-related negativity and its related research

Similar to the response-locked ERN, a stimulus-locked negativity was enhanced when people receive feedback indicating that they have made an incorrect choice or judgment. It was first observed by Miltner and his colleague (1997) in a time-estimation task, in which subjects had to estimate a certain period of time (e.g., one second) before they received accuracy feedback about their estimation. Like the response-locked ERN, this negativity is maximal over medial frontal scalp locations, and source localization analyses suggested the anterior cingulate cortex as the likely generator (Miltner et al., 2003; Ridderinkhof et al., 2004). Miltner et al. (1997) originally proposed that the feedback negativity, similar to the ERN, reflected the operation of an error-processing system, so sometimes the error-related negativity after error feedback is also called the feedback ERN, comparable to the classic response-locked ERN. Moreover this feedback negativity has been also observed in gambling tasks when people make a choice and then receive a *loss* rather than *gain* feedback about their choice (Gehring & Willoughby, 2002; Hajcak et al., 2005a; Yeung et al., 2005; Yeung & Sanfey, 2004). This negativity, together with the feedback-related ERN, is called the feedback-related negativity (FRN).

3.1 Reinforcement learning theory of the ERN

Building upon the error-detection theory, Holroyd and Coles (2002) proposed the reinforcement-learning theory of the ERN (abbreviated RL-ERN) to incorporate both the FRN and the response-locked ERN into a unified theoretical framework. Specifically the RL-ERN theory proposed a motor control system, involving the anterior cingulate cortex, generating behavior appropriate to the task situation, and a monitoring system, located in the basal ganglia, evaluating the discrepancy between the efference copy of the response and the expectation which could be developed according to the history of prior reinforcement associated with a response. Error signals are produced when the basal ganglia find that events are 'worse' than expected, and then further carried by the mesencephalic dopamine system to the anterior cingulate cortex to adjust the task performance, and back to the basal ganglia to improve the predictions.

An important prediction of the RL-ERN theory is that the monitoring system responds to the earliest predictor of error information. Hence in choice reaction time tasks, the ERN was elicited immediately following an erroneous response, and in feedback tasks as the time-estimation paradigm of Miltner et al. (1997), the FRN was observed after the onset of the negative feedback. Furthermore, it has been observed that the FRN amplitude varies inversely with response ERN amplitude as a function of learning in the probabilistic learning paradigm where subjects are required to learn stimulus-response mapping using external feedback (Holroyd & Coles, 2002; Nieuwenhuis et al., 2002; Nieuwenhuis et al., 2005b). During the initial stages of learning, the error signal tends to be elicited by feedback stimuli since subjects have not learned the stimulus-response mappings; as learning progresses, the error signal is slowly "propagated back" from the feedback to the response when the contingencies between stimuli and response are learned. However, the idea that FRN reflects a process of performance monitoring and/or learning about recently executed actions has been challenged by research findings that an FRN was observed following negative outcomes even in a task context in which participants made no overt response (Yeung, Holroyd & Cohen, 2005). Instead, the amplitude of the feedback negativity was correlated with participants' subjective ratings of involvement in the tasks, suggesting that the FRN may reflect the evaluation of the motivational significance of ongoing events (cf. Gehring & Willoughby, 2002).

The RL-ERN theory asserted that the FRN represents the detection of unexpected, unfavorable outcomes (Holroyd & Coles, 2002). Therefore it would predict (1) the FRN effect should be larger for unexpected outcomes than for predicted outcomes; (2) the FRN following unfavorable feedback should be larger for favorable feedback. Empirical studies are reviewed in next section in the light of these two predictions.

3.2 The FRN and the reward expectancy

Several lines of research have been devoted to testing the contention that the FRN reflects a reward prediction error signal. For example, in the probabilistic learning paradigm introduced above, the largest FRN was associated with the most unexpected penalty on trials where participants receive feedback that was inconsistent with learned stimulus-response mappings (Nieuwenhuis et al., 2002; Nieuwenhuis et al., 2005b). Furthermore, by analyzing sequential effects in the random stimulus-response mapping condition, a larger FRN was observed on trials when a feedback stimulus disconfirms a prediction induced by a previous feedback stimulus compared to when the feedback stimulus confirms the prediction (Holroyd & Coles, 2002), suggesting that the FRN amplitude tracks the prediction error on a trial-trial basis.

In addition, Holroyd et al. (2003) manipulated feedback frequency in a gambling task, and found that the FRN amplitude was larger when the negative outcomes (e.g., absence of reward in that study) were infrequent (25%) compared to when they were frequent (75%). According to the RL-ERN theory, the monitoring system in the basal ganglia expects reward when the reward is frequent, and thus the non-reward feedback, inconsistent with this expectation, led to large FRNs; in contrast, the non-reward feedback in the condition when the non-reward feedback is frequent elicited small ERNs because these non-rewards were consistent with the system's expectation. However, Hajcak et al. (2005a) failed to find an influence of reward frequency on the FRN amplitude in their experiments.

A recent study (Hajcak et al, 2007) by the same group of researchers suggested that in order to observe the expectancy effect on the FRN amplitude, subjects' prediction/expectation and their received outcome have to be closely coupled. The reason that the FRN amplitude was not found to be sensitive to the reward probability manipulation may be that the objective probability corresponded too loosely to the subjects' actual expectation. In their 2007 study, they manipulated the reward probability information on a trial-by-trial basis as in Experiment 1 of their 2005 study. They observed a larger FRN upon violations of subjects' reward prediction, when the predictions were made following their gambling choice and right before the feedback, rather than when the predictions were made prior to their gambling choice. Furthermore, it was observed that the predictive cue influenced subjects' predictions regarding the subsequent feedback. However, it differed substantially from objective probability. In general subjects overestimated rewards on 2- (50% predictive) and 3-cue (75% predictive) trials by subjectively predicting rewards around 74% and 95% of trials respectively in one experiment and around 69% and 95% of trials respectively in the other experiment.

3.3 The FRN and feedback favorability

The RL-ERN theory proposed that the FRN reflects an evaluation of events along a general good-bad dimension (Holroyd et al., 2002). The theory is nonspecific about what actually constitutes a good or bad outcome. In fact, Holroyd and colleagues (2004) found that in the gambling task the favorability of each outcome was determined by the context in which the outcome was delivered. For example, feedback indicating that participants received nothing generated a larger FRN in a task situation where participants were supposed to win money, but the same feedback did not generate an FRN in a task context where participants were expecting to lose money.

While the RL-ERN theory does not distinguish between "utilitarian" feedback (e.g., financial rewards and punishment) and "performance" feedback (e.g., performance correctness or error), Gehring and Willoughby (2002) reported that the FRN was sensitive to feedback stimuli indicating monetary gain or loss rather than performance correctness or error. Participants in that study performed a gambling task, in which they were asked to choose one of two squares containing 5 and 25, indicating US cents. Then they received the feedback on both the monetary gain/loss that resulted from the choice, and the monetary gain/loss that would have resulted from making the other choice. Gain or loss information was indicated by color, e.g., red indicating a gain and green indicating a loss. Correctness was defined as whether the chosen outcome was better or worse than the unchosen one, for example, a gain of 5 indicated an incorrect choice if the unchosen alternative was a gain of 25 and a loss of 5 indicated a correct choice if the unchosen alternative was a loss of 25. In addition to these "gain-and-error" and "loss-and-correct" conditions, there were "gain-and-correct" and "loss-and-error" conditions. The ERP waveforms showed that the FRN was not enhanced by error feedback.

Nieuwenhuis et al. (2004b) argued that in Gehring and Willoughby (2002)'s study, the gain-loss information was easier to extract from the feedback display than the correct-error information because the reward information was directly indicated by salient colors but the correctness status was computed by comparing the two numbers and their related colors, which was more attention demanding and time consuming. Thus it is possible that the human monitoring system only responds to the most salient information in the environment about whether the outcomes are good or bad. In their first experiment, they adopted the paradigm used in Gehring & Willoughby (2002), that is, gain-loss information was denoted by colors (e.g., one color indicated gain and the other color indicated loss) and correct-error information was computed by comparing the two numbers and their related colors. In their second experiment, correct-error information was emphasized by color (e.g., one color indicated correct choices and the other color indicated error choices) and gain-loss information was only indicated by plus (+) or minus (-) symbol. They repeated the findings of Gehring & Willoughby (2002) in their first experiment; that is, the FRN was sensitive to the gain-loss information rather than the correct-error information. However, in their second experiment where correctness was indicated by more salient information, the FRN was found to be sensitive to correct-error rather than gain-loss information, suggesting that the FRN may reflect the activity of a single monitoring system that rapidly evaluates outcomes along a good-bad dimension on the basis of the most salient evaluative information in the environment.

3.4 The FRN and binary versus scale evaluation

In the past 4-5 years, increased interest has been devoted to investigating how the system that generates the FRN evaluates outcomes with intermediate values when a range of outcomes is possible. RL-ERN theory would predict that FRN scales with the goodness of ongoing events—intermediate outcomes should be associated with intermediate-sized ERN amplitudes (Holroyd & Coles, 2002; Nieuwenhuis et al., 2004a review). However, an apparent discrepancy with this prediction was found in Holroyd and colleagues (2004)'s study which included a worst, middle and good reward information. In that study, the FRN amplitude elicited by the worst and middle outcomes were not significantly different from each other. The researchers suggested two possible interpretations: (1) the study lacked sufficient statistical power to detect the difference between worse and middle outcomes; (2) the evaluation system that produced the FRN is non-linear, weighing the worst and middle outcomes equally. The latter possibility has been supported by a series of subsequent studies.

Yeung and Sanfey (2004) used a gambling task in which subjects could gamble a small or large amount of money on each trial. They found that loss feedback elicited a larger FRN than gain feedback, however, the amplitude of the FRN was not affected by the magnitude of reward, suggesting that the FRN is related to a simple bad versus good binary appraisal. Nieuwenhuis et al. (2004a) argued that in Yeung & Sanfey's experiment, subjects knew they gambled on a small or large outcome before they made a choice and received the feedback, so their monitoring system may scale its response to the negative feedback by normalizing the extreme outcome. Hajcak and colleagues (Hajcak et al., 2006) avoided this issue by presenting several identical doors for subjects to choose and simply manipulating the reward valence (gain vs. loss) and magnitude (5 vs. 25) of the delivered feedback stimuli in two gambling tasks. Consistent with Yeung and Sanfey's (2004) observation, the FRN amplitude was found insensitive to the graded value of feedback. However, Hajcak et al. (2006) had its own problem, which will be addressed a little later.

Holroyd, Hajcak and Larsen (2006) presented a series of five experiments (four gambling tasks and one estimation task) to investigate the FRN response to neutral feedback stimuli. There were two types of neutral feedback stimuli: one indicated that participants did not receive the potential reward or punishment; the other is uninformative about the feedback outcome although subjects could be either successful or unsuccessful on those trials. Across the five experiments, neutral feedback had consistently elicited an FRN about as large as that elicited by negative feedback stimuli, suggesting that the evaluative system that yielded the FRN classified outcomes works in a binary manner—there are two discrete categories: outcomes indicating the task goal has been satisfied, and everything else. Furthermore, they incorporated these results into the RL-ERN theory by adding a cognitive preprocessing system before the monitoring system in the basal ganglia. The cognitive system establishes the task goal (e.g., earn as much money as possible), and produces output to the monitoring system about whether or not the goal has been satisfied. Correspondingly, the adaptive critic model in the monitoring system computes a binary value which is further communicated to the control system. When the negative and neutral feedback stimuli are grouped into a single category by the cognitive system, the RL-ERN theory would predict equally larger FRNs to the negative and neutral feedback.

4. The FRN and the perceptual mismatch hypothesis

As reviewed before, the FRN got its name because it is a negative voltage deflection often observed following unfavorable feedback stimuli. It has also been called a variety of other names such as the ERN (e.g., Holroyd et al., 2004), the feedback ERN (Miltner et al., 1997) or the medial frontal negativity (e.g., Gehring & Willoughby, 2002). It may also be called an N2, since it is the second negative component on the ERP grand average waveform elicited by the feedback stimuli, and peaks around 200-300 ms after the onset of the feedback stimuli like other N2 components. In particular it may be a part of anterior N2, considering that it has a medial frontal scalp distribution and may originate from the ACC and its neighboring brain regions.

The history of the FRN's discovery (from the ERN) and its extant theoretical framework (RL-ERN theory) have naturally led researchers to make connections between the FRN and general cognitive control functions embodied by the anterior cognitive control N2. In the following paragraph, special review is given to a handful of studies investigating the relationship between the FRN and the perceptual mismatch hypothesis.

Very few studies have investigated the role of perceptual mismatch in the FRN, with some exceptions like the Donkers, Nieuwenhuis and van Boxel (2005) study. In their study, they used a slot-machine task, in which participants were asked to watch three digits presented successively on a computer screen. Three trial types were defined according to the order that those digits appear: type XXX, in which all three digits were identical (e.g., 2 2 2), type XXY, in which the last digit was different from the first two (e.g., 2 2 3), and type XYZ, in which all digits were different (e.g., 2 0 8). The task was run in two conditions: a gain condition, in which participants won a small amount of money if (and only if) the three digits were identical, and a loss condition, in which participants lost a small amount of money when the three digits were identical. For type XXY and XYZ, participants did not win or lose any money. This design was designed to study brain activity associated with both averted gains and averted losses in the complete absence of responding. However, the results, by comparing the ERP waveforms elicited by the last digit of the sequence among the three trial types, revealed that an FRN-like negativity was elicited whenever a stimulus was different from the preceding stimulus, regardless of relative gain or loss. A further investigation (Donkers & van Boxtel, 2005) in which overall frequency of obtaining gains or losses were manipulated, replicated the experimental finding. For example, a larger anterior negativity was still observed in XXY trial type than in XXX trial types in both the gain and loss conditions, although this mismatch effect was larger in the loss condition than in the gain condition. It appears that both the perceptual mismatch and the reward valence affected the FRN observed in this type of study.

In many previous FRN studies, investigators tended to assume that the perceptual properties of the feedback stimuli were not important in determining these feedback effects (Holroyd et al., 2002; Holroyd et al., 2003; Miltner et al., 1997; Hajcak et al., 2006). Indeed, in many ERP and fMRI studies the perceptual properties of the feedback stimuli were confounded with reward valence effect. Considering the evidence that the perceptual salience of the feedback stimuli affect the FRN elicitation (Nieuwenhuis et al., 2004b), as well as the research finding that feedback stimuli whose perceptual attributes mismatch the prepared/primed representation affect the FRN amplitude (Donkers et al., 2005, 2005), it seems that the perceptual attributes of the feedback stimuli may play an important role in the elicitation of the FRN. Research findings from studies which ignored such perceptual attributes may need to be reevaluated. For example, Hajcak et al. (2006)'s study used "++", "+", "-", and "--" to indicate large gain (gain 25 cents), small gain (gain 5 cents), small loss (lose 5 cents) and larger loss (lose 25 cents) feedback respectively, and found a larger FRN after the loss feedback than after the gain feedback, but there was no FRN difference between large and small reward values either in the gain or loss condition. They used these results to support the binary view on the evaluation system that elicits the FRN. The arrangement of their feedback stimuli (the two feedback stimuli indicating large and small outcomes were similar to each other), however, may pose problems for their conclusion in that (1) the perceptual similarity between the two reward stimuli may mask the magnitude effect on the FRN, or (2) all of their FRN findings may be based on the detection of perceptual mismatch from the gain-related feedback, rather than on the detection of "worse than expected" signal as RL-ERN theory claimed.

As Folstein and van Pettern (2008) pointed out, the RL-ERN theory could be a kind of mismatch detection hypothesis, except that the mismatch is occurring between an internal expectation and an external event, rather than between two external events as seen in a typical sequential matching task (Wang et al., 2003). In particular, several studies (Hajcak et al., 2007; for a review, see Krizan & Windschitl, 2007) have shown that subjects in gambling tasks have a positive bias, expecting positive outcomes about their choice. So it is possible that in the gambling task the human perceptual system is tuned for the perceptual attributes of the gain stimuli (e.g. certain gain-related feature(s)), and the feedback outcome that is actually delivered is compared with this primed/prepared gain-related perceptual representation; and any violation of or mismatch from this tuning would trigger the monitoring system to elicit the error signal. Under this perceptual mismatch hypothesis, the monitoring system could produce the error signal very efficiently, consistent with the early latency (200-300 ms) of the FRN following the onset of the feedback stimuli. It is also reasonable to assume that the monitoring system is only responsive to the most salient dimension of the feedback stimuli as shown in Nieuwenhuis et al. (2004b)'s study, because the detection of the salient feedback and its possible mismatch from the perceptual-tuning in the perceptual system will be very fast and the FRN may be sensitive to this fast operation. Indeed, it is doubtful that the human brain could always compute so fast that it knows the outcome is “worse than expected” within 200-300 ms after the feedback. The brain, instead, may use this simpler and faster perceptual mismatch comparison mechanism.

5 Current Research

In this dissertation research, a series of experiments was designed to investigate the role of perceptual mismatch in the elicitation of the FRN. In all seven ERP experiments, simple gambling tasks were used, in which participants made choices among two, three or four boxes, doors or chips presented on the screen, and then received the reward feedback about their choice. Perceptual properties of the feedback stimuli were manipulated.

In some experiments (Experiment 1, 5, 6 and 7), the flanker letter string used in the classical Eriken flanker letter task (Eriken & Eriksen, 1974) was used to indicate the reward information. As in the classic response-time flanker task, this flanker gambling task consists of both congruent and incongruent letter strings. In the congruent letter string, the central target letter and its surrounding flanker letters are identical, conveying consistent reward information (gain, neutral or loss); in the incongruent letter string, the central target letter and its surrounding flanker letters are different, and they convey inconsistent reward information. Participants were instructed that only the reward information conveyed by central target letter was valid. The flanker gambling task defines two types of mismatch: external mismatch, which is present in the external feedback stimuli, specifically the incongruent flanker string (e.g., HHSHH) of the classical Eriksen letter flanker task; and internal mismatch, which is occurring between an external event and a mental template, i.e. the feedback representation actually delivered to the participants versus the perception-tuning prepared in their perceptual system.

By using this flanker letter string, (1) it is possible to investigate whether the presence of the flanker letters (especially in the incongruent flanker letter string) may affect the detection of the reward information and the elicitation of the FRN. For example, the perceptual mismatch hypothesis would predict that the incongruent gain feedback may elicit a larger FRN than congruent gain feedback for two reasons— the increased internal mismatch because of the presence of the loss-related perceptual features and the external mismatch between the gain target and loss flankers in the feedback stimulus itself. The original RL-ERN theory would not predict an enhanced FRN for the incongruent gain because it would still be categorized as a favorable outcome. Furthermore through manipulating the perceptual similarity between the gain and loss information, it is possible to investigate how the FRN may be affected (2) by the degree of the perceptual mismatch between the actual outcome and the prepared mental template in the perceptual system (internal mismatch), and (3) by the degree of the perceptual mismatch existing in the external feedback stimuli (external mismatch). For example, according to the perceptual mismatch hypothesis, the reward information indicated by perceptually very different feedback stimuli would generate a larger FRN reward effect than the reward information indicated by perceptually very similar feedback stimuli (corresponding to purpose 2); the incongruent letter string composed of perceptually very different letters would generate a larger FRN congruency effect than that composed of perceptually very similar letters (corresponding to purpose 3). The current RL-ERN theory would not predict any effect described above.

In other experiments (Experiment 2, 3, 4), a single *color* or *shape* or *letter* was used to indicate the reward information. By using these single objects, first, it is possible to evaluate the contribution of perceptual salience to the FRN (for example, red and blue colors are perceptually more salient than letter E and F when indicating gain or loss feedback information), second, it is possible to directly examine how the FRN may be modulated by the ease of detecting the perceptual mismatch(for example, the processing of a single feature is automatic and fast and the processing of conjoined features is slow and requires attention, so that the FRN elicited by the conjoined features may be later and smaller), and third, it is possible to investigate the contribution of perceptual mismatch between the actual outcome and the expected mental template (internal mismatch) by manipulating the similarity of these single object stimuli which may indicate different reward information (equivalent to purpose 2 in above paragraph), e.g., E and F are more similar to each other than S and T to each other.

The seven experiments formed three sets described in the following three chapters. In the three experiments that comprise Chapter II, the perceptual attributes of gain and loss feedback stimuli were manipulated to provide the basic evidence that the FRN could be affected by the perceptual salience of the feedback stimuli, by the internal perceptual mismatch between the actual outcome and the prepared mental template in the perceptual system, and by the external perceptual mismatch existing in the feedback stimuli. In the three experiments that comprise Chapter III, the perceptual attributes of the neutral feedback stimuli were manipulated to further investigate how both the internal and external perceptual mismatches may affect the FRN elicited by this non-reward or intermediately reward feedback. In the last experiment, comprising Chapter IV, a task-irrelevant feedback condition was included to evaluate the nature of the external perceptual mismatch existing in the feedback stimuli.

Additionally in all seven experiments, the effects of all the experimental manipulations described above have also been evaluated with regards to the P300, as it has been shown to be sensitive to expectancies in numerous tasks (Courchesne, Hillyard, &Courchesne, 1977; Duncan-Johnson & Donchin, 1977; Johnson & Donchin, 1980). Furthermore, some studies have reported that feedback stimuli indicating the outcome of monetary gambles elicited a P300 that was sensitive to the amount of money won or lost rather than the reward valence (Yeung & Saney, 2004; Sato et al., 2005). Other studies showed that the P300 was enhanced by gain feedback in the simple gambling task (Hajcak et al., 2005a, 2007). Still another study (Ito et al., 1998a) reported that a larger P300 was observed in response to affectively negative images than in response to positive images that were matched according to subjective rating of arousal, suggesting that the P300 was sensitive to the negative emotional content of stimuli. It remains undetermined whether the enhancement of P300 amplitude in gambling tasks is due to increased attention or motivation, or whether it encodes some specific information related to reward magnitude or valence.

Chapter II Experiment 1-3

Through the three experiments in this chapter, it is expected to establish the basic evidence on whether the FRN can be affected by the perceptual salience of the feedback stimuli, the perceptual similarity between gain and loss outcomes, and the presence of interference information in the feedback stimuli

Experiment 1: EFST flanker gambling task

Design and Rationale

In Experiment 1, the perceptual properties of the feedback stimuli were manipulated to investigate how the perceptual mismatch between the actual outcome and the prepared mental template in the perceptual system could contribute to the elicitation of the FRN, and how the perceptual mismatch existing in the feedback stimulus itself may contribute to the elicitation of the FRN.

A flanker gambling task was developed and used. In the task, participants made a choice, and then received a classical five-letter flanker string (e.g., TTSTT) as the reward feedback about their choice. In the five-letter flanker string, only the central letter conveyed the reward information about participants' choice. The four surrounding letters were the same to each other, being either identical to (i.e., congruent condition) or different from (i.e., incongruent condition) the central letter. In this way four types of reward feedback existed: *congruent-gain* feedback, in which the central letter indicated a gain, and the flanker letters were identical to the central letter (e.g., TTTTT); *incongruent-gain* feedback, in which the central letter indicated a gain, and the flanker letters were different from the central letter (e.g., SSTSS); *congruent-loss* feedback, in which the central letter indicated a loss, and the flanker letters were identical to the central letter (e.g., SSSSS); and *incongruent-loss* feedback, in which the central letter indicated a loss, and the flanker letters were different from the central letter, e.g., TTSTT. The inclusion of the incongruent-gain and incongruent-loss feedback provides a way to test whether the FRN may be affected by the external perceptual mismatch exisiting in the feedback stimuli.

Furthermore, the similarity of letters indicating *gain* or *loss* feedback was manipulated. In one condition, gain and loss were indicated by two perceptually very similar letters (e.g., *E* or *F*); and in the other condition, gain and loss were indicated by two perceptually dissimilar letters (e.g., *S* or *T*). By comparing the reward effect (gain vs. loss) in these two conditions, it is possible to test whether the FRN may be affected by the degree of the perceptual mismatch between gain- and loss-related feedback representations. In addition, by comparing the congruency effect (congruent vs. incongruent) in these two conditions, it is possible to test whether the FRN may be affected by the degree of perceptual mismatch in the feedback stimuli.

Methods

Participants

There were twelve participants (six males and six females) aged between 18 and 23. All were right-handed, had normal or corrected-to-normal vision, and normal color vision. Prior to the test, participants provided written informed consent in accordance with the Institutional Review Board of the University of Michigan. They received a monetary payment for their participation.

Procedure

The participants were seated comfortably 60 cm in front of a fourteen-inch CRT computer monitor in a dimly lit, sound-attenuating and electromagnetically shielded room. They were instructed to remain as still as possible and to minimize eyeblinks throughout the experiment. Materials were presented using E-prime (Psychological Software Tools, Pittsburgh, PA). On each trial of the experiment (see Figure 2.1 for an example), the participants were presented with four identical red doors shown on the screen following a 500 ms central fixation, and were instructed that the reward information was hidden behind those doors. Doors remained on the screen until the participants selected one of them by pressing its corresponding button with their left or right index or middle finger. One thousand milliseconds after their response, the reward information indicating whether they won or lost on the trial came up and was present for 1000 ms. The inter-trial interval (ISI) was 1000 ms.

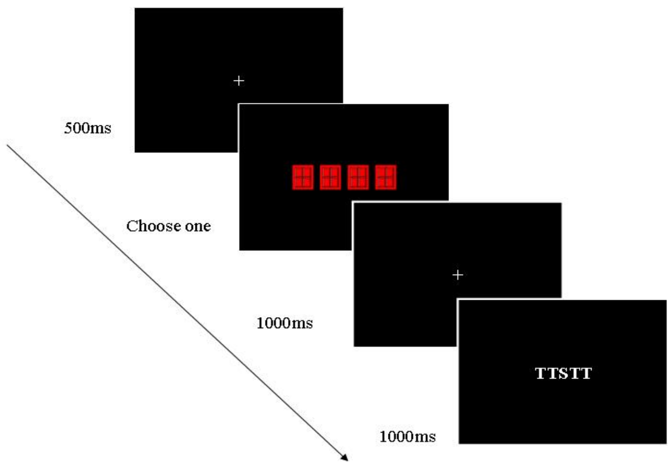


Figure 2.1. A schematic representation of Experiment 1.

The reward information was a letter string in the form of the flanker stimuli— one target letter (e.g., letter S) at the center was surrounded by identical (e.g., SSSSS; *congruent* condition) or different letters (e.g., TTSTT; *incongruent* condition) and only the central letter conveyed the reward information. The perceptual similarity between target and flanker letters was manipulated. In half of the trials, *gain* and *loss* information were indicated by two perceptually similar letters: E vs. F; in the other half of the trials, *gain* and *loss* information were indicated by two perceptually dissimilar letters: S vs. T. Participants completed five sets of EF feedback ('SIM' sets) and five sets of ST feedback ('DIS' sets) with 120 trials in each set. For half of the participants, SIM sets were presented first; and for the other half, DIS sets were presented first. Each set started with 50 cents as the initial allotment, and for each trial participants won or lost 25 cents. They were given summary information about the bonus they had earned every twelve trials. The reward information each letter indicated was revealed to the participants at the beginning of the experiment and was counterbalanced among the participants. The feedback stimuli used in Experiment 1 are shown in Table 2.1. The feedback was randomly chosen from a set of equal numbers of congruent and incongruent as well as gain and loss feedback. On average, the percentage of gain or loss was approximately 50% and the ratio of congruent-to-incongruent trials was roughly 1:1.

	Reward Valence	**Congruency**	**Type name**	**Feedback Stimuli**
Similar	Gain	Congruent	Sim_Gain_con	EEEEE
	Gain	Incongruent	Sim_Gain_inc	FFEFF
	Loss	Congruent	Sim_Loss_con	FFFFF
	Loss	Incongruent	Sim_Loss_inc	EEFEE
Dissimilar	Gain	Congruent	Dis_Gain_con	SSSSS
	Gain	Incongruent	Dis_Gain_inc	SSTSS
	Loss	Congruent	Dis_Loss_con	TTTTT
	Loss	Incongruent	Dis_Loss_inc	TTSTT

Table 2.1. Experiment 1 example of the feedback stimuli.

Electrophysiological Methods

The electroencephalogram (EEG) was recorded from 26 scalp electrode sites with Ag/AgCl electrodes embedded in a nylon mesh cap (Easy-Cap, Falk Minow Systems, Inc., http://www.easycap.de). The electrode locations consisted of FP1, AFz, FP2, F7, F3, Fz, F4, F8, FC3, FCz, FC4, T7, C3, Cz, C4, T8, CP3, CPz, CP4, P7, P3, Pz, P4, P8, O1 and O2. EEG data were recorded with a left mastoid reference and a forehead ground. An average mastoid reference was derived off-line using right mastoid data. The electro-oculogram (EOG) was recorded from Ag/AgCl electrodes above and below the left eye and external to the outer canthus of each eye. Impedances were kept below 10 KΩ. EEG and EOG were amplified by SYNAMPS DC amplifiers (Neuroscan Labs, Sterling, Virginia, USA) and filtered on-line from .01 to 100 Hz (half-amplitude cutoffs). The data were digitized at 500 Hz.

EEG epochs of 1100 ms (100 ms baseline) were extracted off-line from the continuous data file for analysis. Ocular artifacts were corrected using the algorithm described in Gratton, Coles and Donchin's paper (Gratton, Coles & Donchin, 1983). Statistical analyses were performed on the data without any additional filtering. The data presented in the figures were filtered with a nine point Chebyshev II low-pass digital filter with a half-amplitude cutoff at 12 Hz (Matlab 7.04; Mathworks, Natick, MA). For all analyses, *p* values in all main and interaction effects were corrected using the Greenhouse-Geisser method for violations of the sphericity assumption in repeated-measures effects.

Results

The FRN

Figure 2.2 presents the ERPs for *congruent-gain*, *congruent-loss*, *incongruent-gain* and *incongruent-loss* feedback for the similar and dissimilar sets at electrode FCz where the FRN is frequently maximal. The FRN is characterized by the negative deflection that peaked about 300 ms following the feedback.

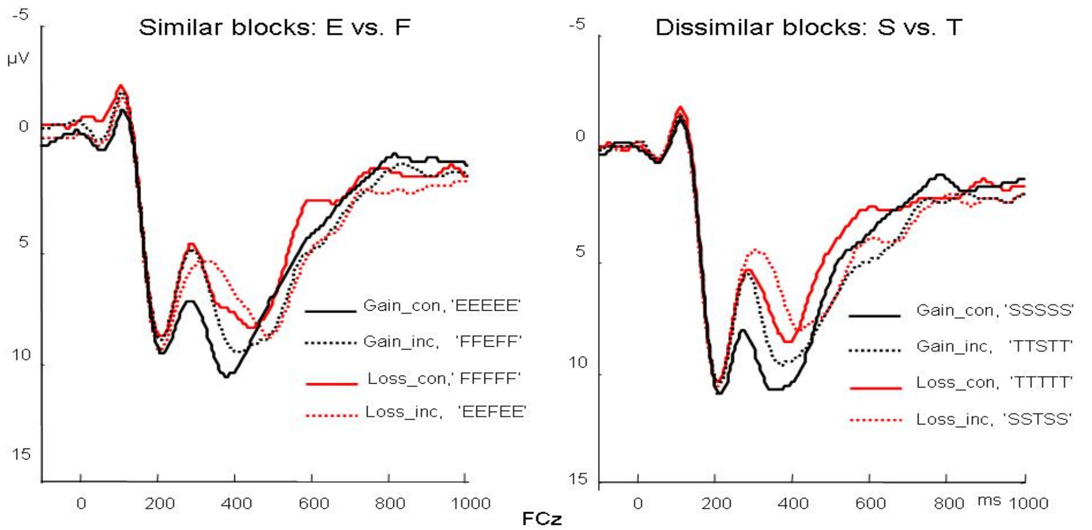


Figure 2.2. Experiment 1 ERP waveforms at electrode FCz. Similar (left, E/F) and dissimilar sets (right, S/T) are displayed separately.

Figure 2.3 and Figure 2.4 present the topographic maps of the FRN between 250 ms and 350 ms following the feedback onset respectively for the *loss-minus-gain* difference waveforms and the *incongruent-minus-congruent* difference waveforms, suggesting a medial-frontal distribution of the FRN. The FRN mean amplitude between 250 ms and 350 ms following the feedback was measured at FCz. A 2×2×2 three-way repeated-measures ANOVA with factors *set type, reward valence* and *congruency* revealed main effects in the reward valence (*gain* vs. *loss*; $F(1, 11) = 19.31$, $p < 0.01$) and the congruency (*congruent* vs. *incongruent*; $F(1, 11) = 9.83$, $p < 0.01$), in addition to an interaction between reward valence and congruency ($F(1, 11) = 8.11$, $p < 0.05$) as well as between reward valence and set type ($F(1, 11) = 5.10$, $p < 0.05$). However, no other main effect or interaction effects were found. In general, *loss* feedback elicited a larger FRN than *gain* feedback, and *incongruent* feedback elicited a larger FRN than *congruent* feedback. Simple-effect analyses showed that the congruency effect was evident only in the *gain* feedback ($F(1, 11) = 14.44$, $p < 0.01$), but not in the *loss* feedback ($F(1, 11) = 2.57$, $p > 0.10$). The reward effect was larger in the DIS sets than that in the SIM sets.

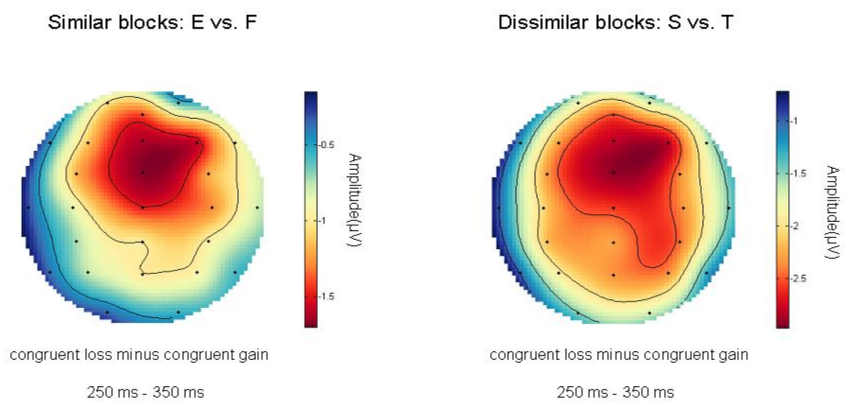


Figure 2.3. Experiment 1 topographic maps of difference waveforms between congruent loss and congruent gain feedback conditions. Similar (left, E/F) and dissimilar sets (right, S/T) are displayed separately.

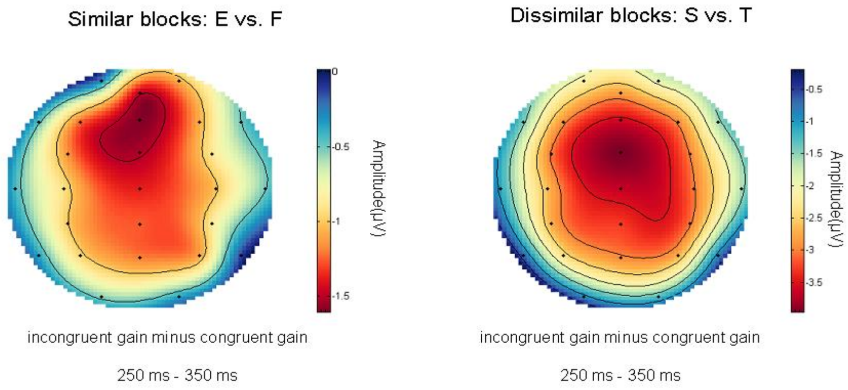


Figure 2.4. Experiment 1 topographic maps of difference waveforms between incongruent gain and congruent gain feedback conditions. Similar (left, E/F) and dissimilar sets (right, S/T) are displayed separately.

Inspection of the ERP waveforms in Figure 2.2 suggested that the mean amplitude analysis using 250-350 ms as the time window may not best catch the late enhancement of the FRN in the *incongruent-loss* feedback condition, so a baseline-to-peak measurement was conducted at FCz as well. The peak amplitude of the FRN was defined as the most negative value of the ERP waveforms between 200 ms and 400 ms following the feedback, and the peak latency of the FRN was defined as the time when the most negative peak occurred. For the peak amplitude analysis, a 2×2×2 three-way repeated-measures ANOVA with factors *set type*, *reward valence* and *congruency* revealed main effects in reward valence (gain vs. loss; $F(1, 11) = 10.12$, $p<0.01$) and congruency (congruent vs. incongruent; $F(1, 11) = 9.52$, $p<.01$), which were consistent with the findings in the mean amplitude analysis. The two interactions that were significant in the mean amplitude analyses became marginally significant in the peak amplitude analyses (reward valence by set type: $F(1, 11) = 4.66$, $p = 0.053$; reward valence by congruency: $F(1, 11) = 4.65$, $p=0.054$). Nevertheless, the interaction between set type and congruency, which was not significant in the mean amplitude analysis, became significant in the peak amplitude analysis ($F(1, 11) = 6.21$, $p<0.05$). Consistent with the analysis of the mean amplitude data, simple-effect analyses of the peak amplitude data showed that the congruency effect was evident only in the *gain* feedback ($F(1,11) = 19.60$, $p<0.01$) but not in the *loss* feedback ($F(1,11) = 1.70$, $p>0.10$), and the reward effect was significant in the DIS sets ($F(1, 11) = 10.28$, $p<0.01$), and marginally significant in the SIM sets (F (1,11) =4.31, p=.06). In addition, the congruency effect was found significant in the DIS sets (F (1, 11) =9.79, p<0.01) but not in the SIM sets (p>0.10).

For the peak latency analysis, the omnibus ANOVA revealed a main effect of congruency (F (1, 11) =8.32, p<0.05). *Incongruent* feedback had a later FRN peak than *congruent* feedback. There were no other main effects or interaction effects (p>0.10)

The P300

The P300 was characterized by the positive waveform enhanced between 300 ms and 500 ms following the feedback as shown in Figure 2.5.

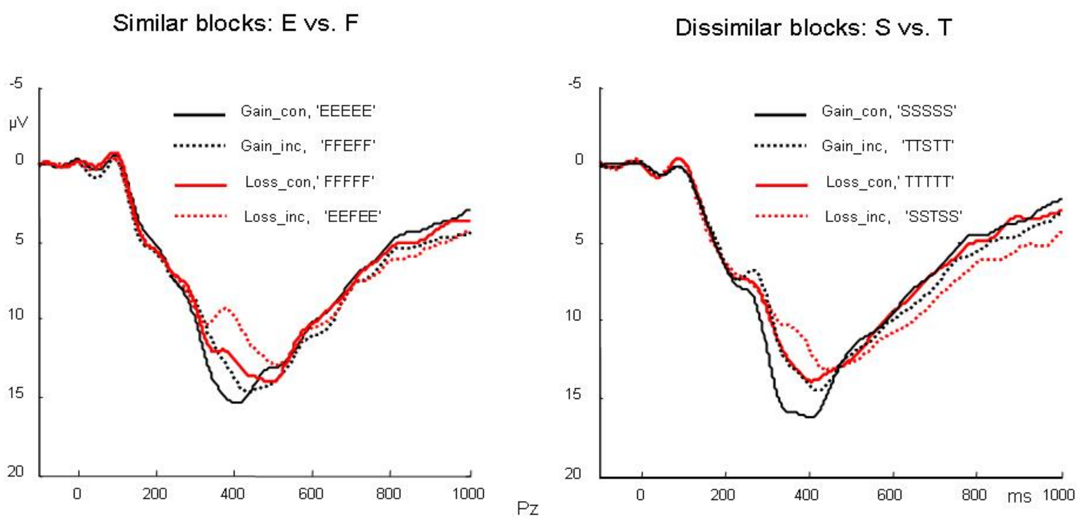


Figure 2.5. Experiment 1 ERP waveforms at electrode Pz. Similar (left, E/F) and dissimilar sets (right, S/T) are displayed separately.

The mean amplitude between 300 ms and 500 ms after the onset of the feedback stimulus was measured at electrode Pz (where the P300 is frequently maximal). A 2×2×2 three-way repeated-measures ANOVA with factors set type, reward valence and congruency revealed main effects in the reward valence (gain vs. loss; F (1, 11) = 14.58, *p*< 0.01) and the congruency (congruent vs. incongruent; F (1, 11) = 11.52, *p*< 0.01).

Gain feedback elicited a larger P300 than *loss* feedback, and *congruent* feedback elicited a larger P300 than *incongruent* feedback. There were no other statistically significant main effects or interactions.

The baseline-to-peak measurement was also conducted: the peak amplitude of the P300 was defined as the most positive value between 300 ms and 600 ms after the onset of the feedback, and the peak latency was defined as the time when the most positive peak occurred. Statistical analyses on the peak amplitude and the peak latency data showed that *gain* feedback elicited a larger ($F(1, 11) = 11.09$, $p<0.01$) and an earlier P300 ($F(1, 11) = 5.36$, $p<0.05$) than *loss* feedback. *Congruent* feedback elicited a larger P300 than *incongruent* feedback ($F(1, 11) = 15.26$, $p<0.01$). There were no other main effects or interaction effects found in these analyses.

Experiment 1 Summary

Experiment 1 results obtained by manipulating the reward valence, congruency and perceptual similarity of the feedback stimuli in a gambling task are summarized as follows. *First*, consistent with previous research reports (Gehring & Willoughby, 2002; Yeung & Safney, 2004; Hajack et al., 2005a), *loss* feedback elicited a larger FRN than *gain* feedback. A *second* and rather unanticipated result according to the RL-ERN theory was that the incongruent *gain* feedback elicited a greater and delayed FRN-like negativity than the congruent *gain* feedback. *Third*, dissimilar-letter feedback had both a larger FRN reward valence effect (i.e., loss minus gain feedback) and a larger FRN congruency effect (i.e., incongruent minus congruent feedback) than similar-letter feedback. *Fourth, gain* feedback elicited a larger and earlier P300 than *loss* feedback, and congruent feedback elicited a larger and earlier P300 than incongruent feedback.

The perceptual mismatch hypothesis could interpret the three FRN results as follows. First, the perceptual system is tuned for gain-related perceptual attributes, and the delivery of the *loss* feedback mismatches this tuning and leads to an enhancement of the FRN in the general *loss* condition. Second, the external mismatch presented in the *incongruent* feedback stimuli could lead to a larger FRN-like negativity in the *incongruent* feedback than in the *congruent* feedback. Third, the larger FRN reward effect and congruency effect shown in the dissimilar letter feedback compared to the similar letter feedback confirm that it is respectively the internal and external perceptual mismatches that lead to the FRN effects rather than other kinds of mismatches, for example, semantic mismatch between gain and loss feedback or between target and flanker letters.

Experiment 2: Single object gambling task

Design and Rationale

In Experiment 2, the perceptual properties of the feedback stimuli were manipulated to investigate how the FRN may be affected by the perceptual salience of the feedback stimuli and the perceptual similarity between gain and loss outcomes. In the experiment, gain and loss reward information were indicated by several pairs of single objects with different perceptual properties, including a pair of colored squares, a pair of irregular shapes, a pair of similar letters and a pair of dissimilar letters. Color and shape were considered as more salient than letters because people can recognize color and shape early before they learn to read. Experimental results found that color is recognized faster than letters (Flowers et al., 2004). Thus it was expected to see an earlier and/or larger FRN effect in response to the salient color and shape feedback than to non-salient letter feedback, because salient information could be processed more efficiently by the monitoring system. Meanwhile, as in Experiment 1, a larger FRN reward effect was expected to be observed on dissimilar letter feedback trials than on similar letter feedback trials because the internal mismatch between the actual outcome and the perceptual tuning in the perceptual system would be larger in the dissimilar letter feedback than in the similar letter feedback.

Methods

Participants

There were twenty-four participants (twelve males and twelve females) aged between 18 and 23. All were right-handed, had normal or corrected-to-normal vision, and normal color vision. Prior to the test, participants provided written informed consent in accordance with the Institutional Review Board of the University of Michigan. They received three-hours-worth of course credit and a three-to-five dollar bonus for their participation. The data from six participants (two males) were excluded from the analyses due to excessive artifacts in the raw EEG data.

Procedure

The participants were seated comfortably 60 cm in front of a fourteen-inch CRT computer monitor in a dimly lit, sound-attenuating and electromagnetically shielded room. They were instructed to remain as still as possible and to minimize eyeblinks throughout the experiment. Materials were presented using E-prime (Psychological Software Tools, Pittsburgh, PA). On each trial of the experiment (see Figure 2.6 for an example), the participants were presented with two identical round chips displayed at the center of the screen following a 500 ms central fixation, and were instructed that one chip included a gain and the other one included a loss. Chips remained on the screen until the participants selected one of them by pressing a button with their left or right index finger, corresponding to the location of the chosen chip. One thousand and eight hundred milliseconds after their response, the reward information indicating whether they won or lost on the trial came up and was present for 1000 ms. The inter-trial interval (ISI) was 1000 ms.

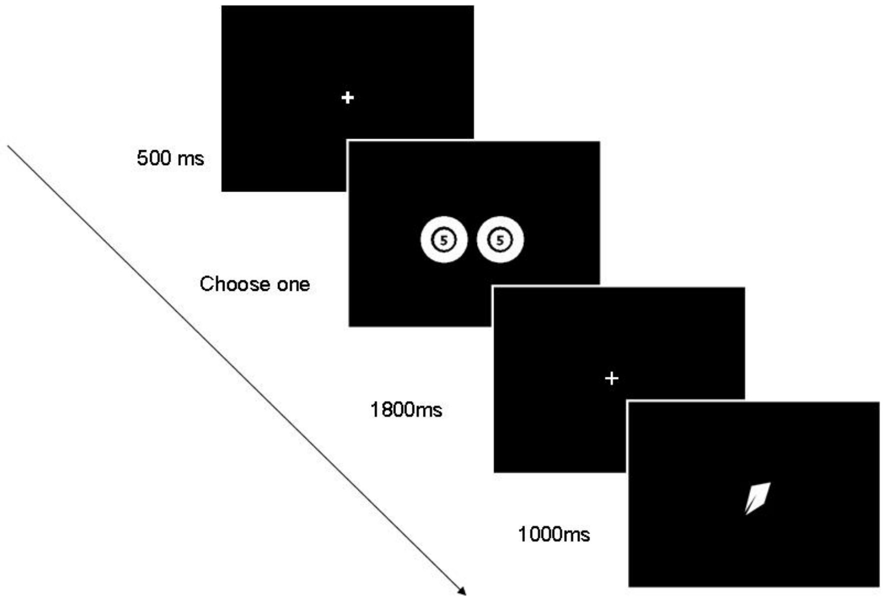


Figure 2.6. A schematic representation of Experiment 2.

The reward information was represented by *color, shape, similar letter* and *different letter* in four types of trial sets respectively. The feedback stimuli used in Experiment 2 are shown in Table 2.2. In the *color* sets, *gain* and *loss* information were indicated by one red and one blue color square; in the *shape* sets, *gain* and *loss* information were indicated by two six-angle Atteneave shapes (Atteneave, 1957) with medium similarity; in the *similar letter* sets, *gain* and *loss* information were indicated by two visually similar letters— E and F; and in the *different letter* sets, *gain* and *loss* information were indicated by two visually different letters— S and T. Participants completed two randomized replicates of four set of trials. Each replicate comprised four trial sets with four different types. All participants completed a total of eight sets. Each set started with 50 cents as the initial allotment, and for each trial participants won or lost five cents. On average the participants received a three-to-five dollar bonus. There were 110 trials for each set, and the participants were given summary information about the bonus they had earned every eleven trials. The reward information each feedback stimulus indicated was revealed to the participants at the beginning of the experiment, and was counterbalanced among the participants. The feedback was randomly chosen from a set of equal numbers of gain and loss feedback. On average, the percentage of gain or loss was approximately 50%.

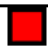
	Reward Valence	**Feedback Stimuli**
Color	Gain	
	Loss	
Shape	Gain	
	Loss	
Similar Letter	Gain	E
	Loss	F
Dissimilar Letter	Gain	S
	Loss	T

Table 2.2. Experiment 2 example of the feedback stimuli.

Electrophysiological Methods

The electrophysiological methods in Experiment 2 were identical to those in Experiment 1.

Results

Behavioral Results

Figure 2.7 presents how frequently participants changed their response depending on the outcome of previous choices. A paired-sample t-test indicated that participants switched their response more frequently when the outcome of their previous choice was a loss (68%) compared to when it was a gain (60%, $p<0.05$), suggesting that participants adjusted their behavior according to the feedback.

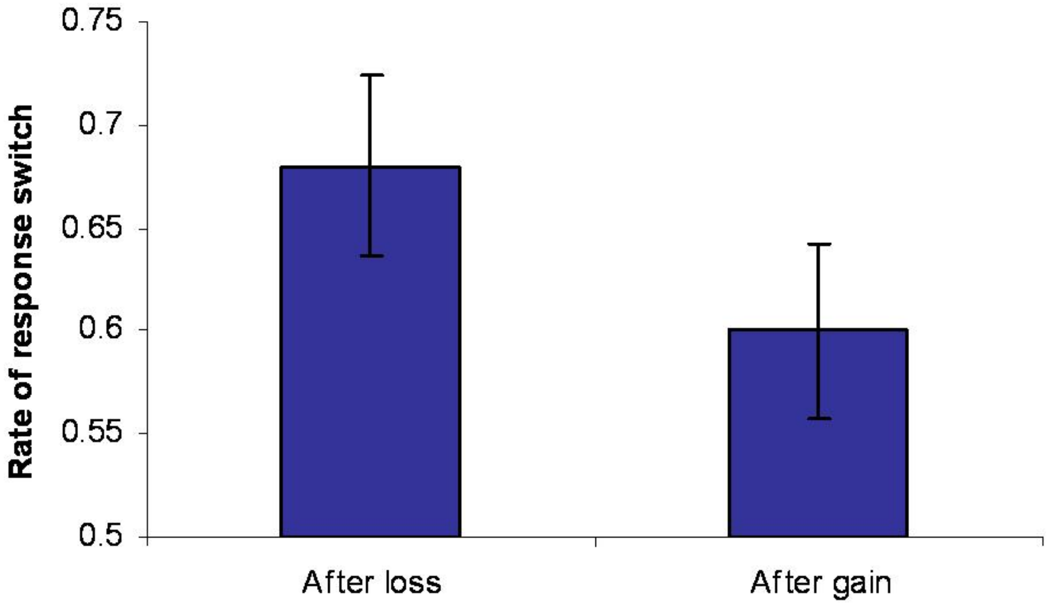


Figure 2.7. Experiment 2 behavioral results.

Electrophysiological Results

The FRN

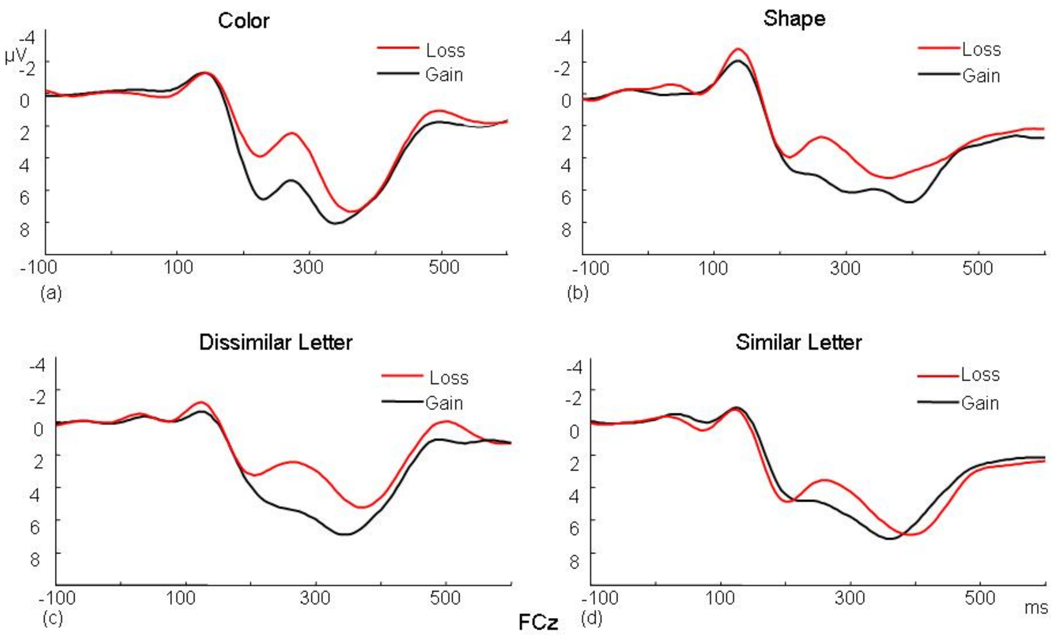


Figure 2.8. Experiment 2 ERP waveforms at electrode FCz. (a) color sets; (b) shape sets; (c) dissimilar letter sets; (d) similar letter sets.

Figure 2.8 presents the ERPs for *gain* and *loss* feedback for the color, shape, similar letter and different letter sets at electrode FCz. The FRN was characterized by the negative deflection that peaked about 200-300 ms following negative feedback. The FRN mean amplitude between 200 ms and 300 ms following the feedback was measured at electrode FCz. A 4×2 two-way repeated-measures ANOVA with factors *set type*(color, shape, dissimilar and similar letter sets) and *reward valence*(gain vs. loss)revealed a main effect in reward valence, $F(1, 17) = 22.09$, $p<.001$. *Loss* feedback elicited a larger FRN than *gain* feedback. There was no interaction between set type and reward valence ($F(3, 51) = 2.29$, $p>.10$). Planned contrasts showed that color and shape sets elicited larger FRN reward effects than similar letter sets ($F(1, 17) = 7.25$, $p<0.05$), but not larger than dissimilar letter sets ($F<1$). In addition a 2×2 two-way repeated-measures ANOVA analyses in the letter feedback sets revealed a marginally significant interaction between set type (similar vs. dissimilar letter) and reward valence (gain vs. loss) ($F(1, 17 = 3.67$, $p<0.10$), suggesting the FRN in the dissimilar sets tended to be larger than in the similar sets.

The P300

The P300 was measured as the mean amplitude between 250 ms and 450 ms after the onset of the feedback stimulus at electrode Pz (see figure 2.9). A 4×2 two-way repeated-measures ANOVA with factors *set type*(color, shape, dissimilar and similar letter sets) and *reward valence*(gain vs. loss)revealed a main effect in reward valence ($F(1, 17) = 20.58$, $p<0.001$) and a marginally significant main effect in set type ($F(3, 51) = 2.70$, $p<.10$). There was no interaction between set type and reward valence ($F < 1$). *Gain* feedback elicited a larger P300 than *loss* feedback. Planned contrasts did not show FRN effect difference between salient and less salient sets ($F < 1$). Similar letter feedback elicited a larger P300 than dissimilar letter feedback.

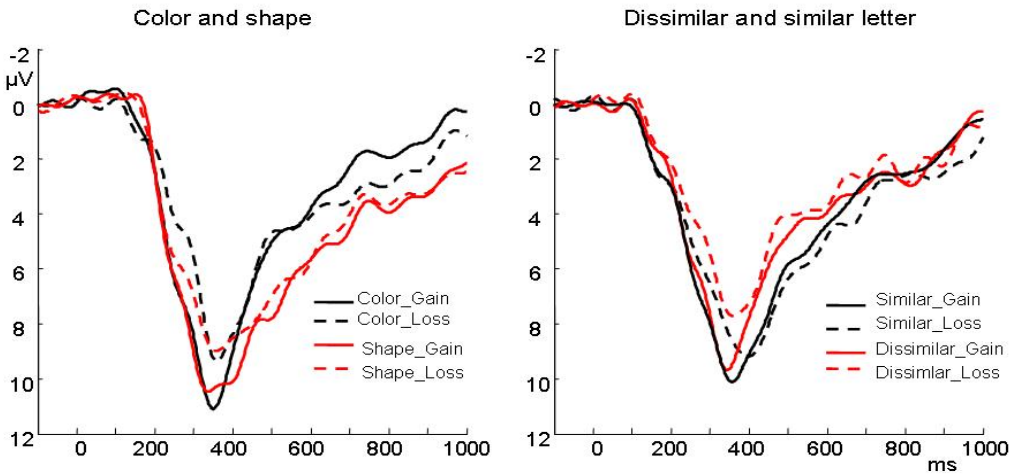


Figure 2.9. Experiment 2 ERP waveforms at electrode Pz. (a) color and shape sets; (b) dissimilar and similar letter sets.

The P300 baseline-to-peak amplitude and the peak latency were measured between 250 ms and 450 ms after the onset of the feedback. As in the P300 mean amplitude analyses, statistics on the P300 peak amplitude revealed a main effect of reward valence ($F(1, 17) = 15.49$, $p<.01$). There was no main effect of set type ($F(3, 51) = 2.41$, $p>.10$) or interaction effect between set type and reward valence ($F<1$). For the peak latency analyses, a 4×2 two-way repeated-measures ANOVA with factors *set type* and *reward* *valence* revealed a main effect in reward valence ($F (1, 17) = 4.89$, $p < 0.05$) and a marginally significant main effect in set type ($F (3, 51) = 2.95$, $p = .057$). There were no interaction effect between set type and reward valence ($F (3, 51) = 1$, $p > .10$). *Gain* feedback elicited an earlier P300 than *loss* feedback. Planned contrasts showed that color and shape sets elicited an earlier P300 than similar and dissimilar sets.

Experiment 2 Summary

Experiment 2 results obtained by using four pairs of feedback with different perceptual properties in a gambling task are summarized as follows. In all the four types of sets, *loss* feedback elicited a larger FRN than *gain* feedback. Participants switch their response choice more often after a *loss* outcome than after a *gain* outcome, suggesting that they knew whether they won or lost during the trial and that they adjusted their behavior on-line according to their received feedback. The FRN reward valence effect in color and shape sets was larger than in similar letter sets, suggesting that the FRN reward valence effect was affected by the perceptual salience of the feedback information. However, the lack of a difference in the FRN effect between color/shape and dissimilar letter sets, may suggest that it is not perceptual salience per se but perceptual mismatch that is responsible for the FRN difference found between color/shape sets and similar letter sets. In addition, consistent with the research finding in Experiment 1, dissimilar letter feedback tended to have a larger FRN reward valence effect than similar letter feedback, suggesting that the FRN reward valence effect was affected by the degree of the perceptual mismatch between the actual outcome and the prepared mental template in the perceptual system. However, this similarity effect on the FRN was only marginally significant in Experiment 2. One possible reason is that perceptually one single letter in this experiment is not as salient as five letters standing together in Experiment 1, and the effect of similarity may be modulated by the salience level, leading to a weaker FRN effect in this experiment.

Overall, gain feedback elicited a larger and earlier P300 than loss feedback, consistent with Experiment 1 findings. Salient feedback elicited an earlier P300 than non-salient feedback.

Experiment 3: Single vs. conjoined feature gambling task

Design and Rationale

Experiment 3 contributed to examining how the FRN may be affected by the ease of detecting perceptual mismatch. In the experiment, either a single feature or a set of conjoined features was designated to indicate *gain* and *loss* reward information in a gambling task. When the reward information was indicated by a single feature, the perceptual mismatch between the actual outcome and perceptual tuning in the perceptual system is easy to detect because the detection of a single feature may rely on the pop-out principle and the comparison between two single features is also very fast. When the reward information was indicated by conjoined features, the perceptual mismatch may be hard or take a long time to detect because the detection of the conjoined feature and the comparison between two conjoined features demand a lot of attention resources according to Treisman's feature integration theory (Treisman & Gelade, 1980). Consequently, it was predicted that the FRN reward effect may be delayed or diminished in the conjoined feature sets than in the single feature feedback.

Methods

Participants

There were nineteen participants (eight males and thirteen females) aged between 18 and 23. All were right-handed, had normal or corrected-to-normal vision, and normal color vision. Prior to the test, participants provided written informed consent in accordance with the Institutional Review Board of the University of Michigan. They received three-hours-worth of course credit and a three-to-five dollar bonus for their participation. The data from six participants (two males) were excluded from the analyses: two participants were excluded because they were too sleepy to conduct the experiment; one participant was excluded because of the wrong operation of the experimenter; two more participants were excluded because of excessive artifacts

Procedure

The procedure in Experiment 3 was same as that of Experiment 1, except that the stimuli used to indicate the reward information were different (see Table 2.3).

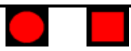
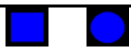
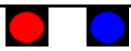
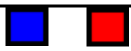
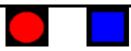
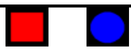
	Reward Valence	**Feedback Stimuli**
Single feature Color	Gain	
	Loss	
Single feature shape	Gain	
	Loss	
Conjoined feature	Gain	
	Loss	

Table 2.3. Experiment 3 example of the feedback stimuli.

In the experiment, four stimuli— red circle, red square, blue circle and blue square, served as the feedback. There were three types of sets: *single feature color sets*, in which the reward information was indicated by a certain color (e.g., *gain* was indicated by red circle and square); *single feature shape sets*, in which the reward information was indicated by a certain shape (e.g., *gain* was indicated by red circle and blue circle); *conjoined color-shape feature sets*, in which the reward information was indicated by conjoined features (e.g., *gain* was indicated by red circle and blue square). Each type of sets had three sets presented together, and the presentation sequence of the three types of sets was counterbalanced among the participants. All other parameters were identical to Experiment 2.

Electrophysiological Methods

The electrophysiological methods in Experiment 3 were identical to those in Experiment 1.

Results

Behavioral Results

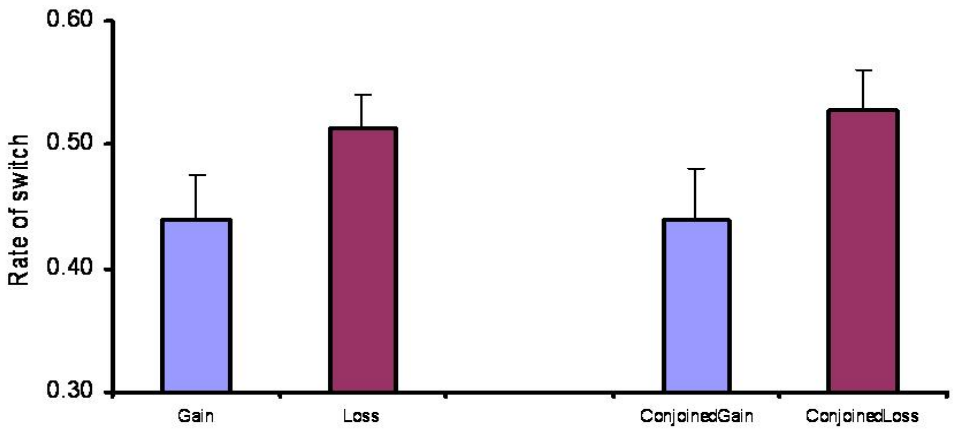


Figure 2.10. Experiment 3 behavioral results. Left, for all sets; right, for conjoined sets.

Figure 2.10 shows that participants switched their response more frequently after *loss* feedback than after *gain* feedback ($p<0.05$). Especially in conjoined feature sets, the switch rate after *loss* feedback was significantly greater than after *gain* feedback ($p<0.01$), suggesting that participants could discriminate *gain* from *loss* even in conjoined feature sets.

Electrophysiological Results

The FRN

As in Experiment 2, the FRN mean amplitude between 200 ms and 300 ms following the feedback was measured at FCz (see Figure 2.11). A 3×2 two-way repeated-measures ANOVA with factors *set type* and *reward valence* revealed main effects in set type ($F(2, 24)=5.01$, $p<0.05$) and reward valence ($F(1, 12)=22.70$, $p<0.01$), in addition to an interaction between set type and reward valence ($F(2, 24)=4.14$, $p<0.05$). Subsequent analyses showed that in single feature sets, *loss* feedback elicited a larger FRN than *gain* feedback ($F(1, 12)=34.05$, $p<0.01$), and there was no main effect or interaction effect related to set type; in conjoined feature sets, there was no difference between *gain* and *loss* feedback (F<1) in the FRN latency window. Inspection of the ERP waveforms in Figure 2.11 suggested a later FRN in conjoined feature sets. However, a mean amplitude between 400 ms and 500 ms as a possible late FRN amplitude was measured for conjoined feature feedback, but there was no significant difference found between *gain* and *loss* feedback (F (1, 12) =1.60, p>0.1)

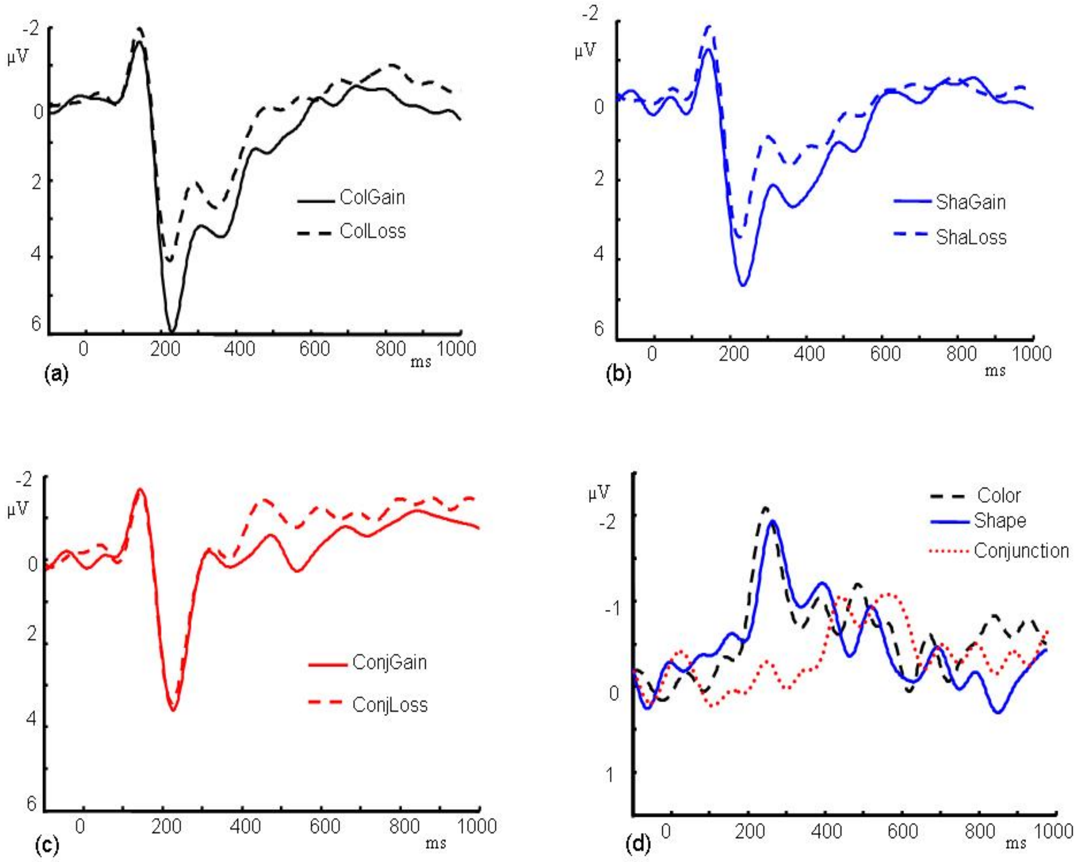


Figure 2.11. Experiment 3 ERP waveforms at electrode FCz. (a) color sets; (b) shape sets; (c) conjoined sets; (d) difference waveforms in the three types of sets.

The P300

The P300 was measured as the mean amplitude between 250 ms and 450 ms after the onset of the feedback stimuli at electrode Pz (see Figure 2.12). A 3×2 two-way repeated-measures ANOVA with factors *set type* and *reward valence* revealed a marginally main effect in reward valence (F (1, 12) =4.02, p=0.068) and a marginally significant main effect in set type (F (2, 24) =3.48, p =0.060), but no interaction effect between set type and reward valence (F<1). Overall *gain* feedback appeared to elicit a larger P300 than *loss* feedback. Conjoined feature sets had a smaller P300 than single feature sets ($F(1, 12) = 12.20$, $p < 0.01$).

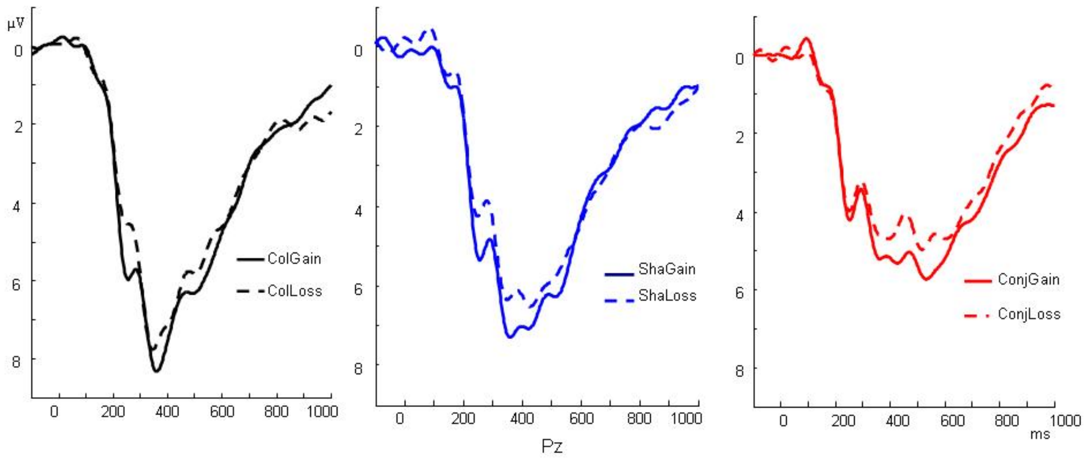


Figure 2.12. Experiment 3 ERP waveforms at electrode Pz. Left, color sets; middle, shape sets; right, conjoined sets

Experiment 3 Summary

Experiment 3 results obtained by using single-feature or conjoined-features reward stimuli in a gambling task are summarized as follows. In single-feature sets, *loss* feedback elicited a larger FRN than *gain* feedback. In conjoined feature sets, there was no difference between *loss* and *gain* feedback in terms of the FRN amplitude, although behaviorally participants switched their response choice more often after a *loss* outcome than after a *gain* outcome in these sets suggesting that participants know whether they won or lost on that trial. Overall *gain* feedback appeared to have a larger P300 than *loss* feedback. Single-feature feedback elicited a larger P300 than conjoined-features feedback.

Chapter II Discussion

In this chapter, three experiments were conducted to investigate how the FRN may be affected by the perceptual properties of the feedback stimuli. It was found that in general, *loss* feedback elicited a larger FRN than *gain* feedback and this FRN reward effect was modulated by the perceptual salience of the feedback stimuli and the perceptual difference between *gain* and *loss* feedback stimuli. Specifically, salient feedback stimuli had a larger FRN reward effect than non-salient feedback stimuli. When the reward information was indicated by conjoined perceptual features rather than single perceptual feature, the FRN reward effect was diminished. One of the most interesting results is that the FRN reward effect was larger when the *gain* and *loss* feedback were indicated by two perceptually different letters compared to when they were indicated by two perceptually similar letters, suggesting that the perceptual similarity between *gain* and *loss* feedback stimuli affected the FRN amplitude. Furthermore, the presence of the flanker letters that were different from the target letter enhanced the FRN-like negativity in the feedback stimuli especially in the gain feedback condition, and this FRN congruency effect was further modulated by the similarity between the target and flanker stimuli.

In the original RL-ERN model, perceptual properties were not considered as a factor contributing to the FRN, although Nieuwenhuis et al.(2004b)'s experiments suggested that the monitoring system may be only sensitive to the most salient dimension of the feedback stimuli. While it is hard for the RL-ERN theory to explain any of the experimental findings described above except that the *loss* feedback elicited a larger FRN than the *gain* feedback, the perceptual mismatch hypothesis can accommodate these results in the following ways.

During the task, the perceptual system was tuned for gain-related perceptual attributes, perhaps because participants hoped to win rather than lose money. When *gain* and *loss* feedback were indicated by single features, mismatch between the actual loss feedback and the gain-perceptual-tuning was easy to detect due to the pop-out characteristic of the single feature, which enhanced the FRN effect. In contrast, when *gain* and *loss* feedback were indicated by conjoined features, the conjoined features were hard to detect since integration of features requires a lot of attention according to the feature integration theory (Treisman &Gelade, 1980). Correspondingly the perceptual mismatch was harder to detect, which led to a delayed or diminished FRN. There are two types of mismatch: one is the mismatch in the external stimuli, e.g., when the flanker letters and the target letter are different, and the other is the mismatch between the actual loss outcome and the gain perceptual tuning in the perceptual system. Each type of mismatch would elicit an FRN-like negativity, and the FRN effects in both cases were found to be sensitive to the degree of perceptual mismatch.

In addition to the FRN effect, it was found that behaviorally participants switch more often after they receive a *loss* feedback compared to when they receive a *gain* feedback, and the FRN effect does not always correspond to this behavioral switch effect. Furthermore, it was observed that a larger P300 was elicited by a *gain* feedback than by a *loss* feedback, and by a congruent feedback than by an incongruent feedback. However both the two P300 effects were not modulated by the degree of the perceptual mismatch, suggesting that the P300 may affect some mental activity after the perceptual mismatch was detected. It was also found that single-feature feedback elicited a larger P300 than conjoined feature feedback.

Chapter III Experiment 4-6

The three experiments in this chapter are dedicated to investigating how the FRN elicited by the neutral outcome in gambling tasks may be modulated by its perceptual similarity to gain/loss feedback and the presence of interference information in the feedback stimuli.

Experiment 4: Shape gambling task

Design and Rationale

In Experiment 4, the perceptual similarity between neutral and gain/loss feedback stimuli were manipulated to examine whether the FRN elicited by the neutral feedback may be affected by this manipulation. In the experiment, some regular shapes were chosen to denote *gain*, *neutral* and *loss* reward information. In some sets, *neutral* and *gain* feedback were indicated by similar shapes, but *loss* feedback was different. In other sets, *neutral* and *loss* feedback were indicated by similar shapes, but *gain* feedback was different. In still other sets, all the *gain*, *neutral* and *loss* feedback were indicated by different shapes. If the perceptual attributes of the feedback stimuli modulated the FRN activity elicited by the *neutral* feedback, it would be expected that the neutral FRN would be smaller when the *neutral* feedback was similar to the *gain* feedback compared to when it was different from the *gain* feedback. If the gain-related feedback rather than the loss-related feedback were primed to be compared to the sensory analysis outcome of the actual received feedback, it would not make much difference in terms of the neutral FRN activity between the sets where *neutral* and *loss* feedback were similar and the sets where *neutral* and *loss* feedback were different.

Methods

Participants

There were seventeen participants (ten males and seven females) aged between 18 and 30. All were right-handed, had normal or corrected-to-normal vision, and normal color vision. Prior to the test, participants provided written informed consent in accordance with the Institutional Review Board of the University of Michigan. They received a monetary payment for their participation

Procedure

The participants were seated comfortably 60 cm in front of a fourteen-inch CRT computer monitor in a dimly lit, sound-attenuating and electromagnetically shielded room. They were instructed to remain as still as possible and to minimize eyeblinks throughout the experiment. Materials were presented using E-prime (Psychological Software Tools, Pittsburgh, PA). On each trial of the experiment (see Figure 3.1 for an example), the participants were presented with three identical chips at the center of the computer screen following a 300 ms central fixation, and were instructed that each chip was associated with gain, neutral or loss feedback information. Chips remained on the screen until the participants selected one of them by pressing its corresponding button with their right index finger. One thousand milliseconds after their response, the reward information came up and was present for 600 ms. The inter-trial interval (ISI) was 300 ms.

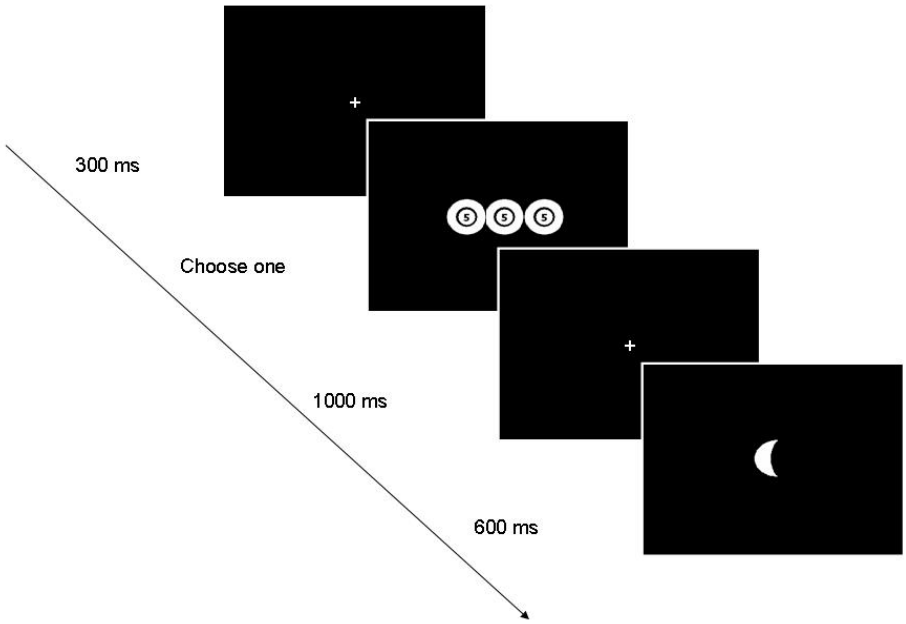


Figure 3.1. A schematic representation of Experiment 4.

The reward information was indicated by different simple shapes. There were three types of sets, where the similarity of the shapes indicating *gain*, *neutral* and *loss* were manipulated (See Table 3.1). In one type of sets, *gain*, *neutral* and *loss* feedback were indicated by three different shapes, e.g., first quarter moon ( ), equilateral triangular ( ), and cross ( ). In another sets, called L sets, the shape indicating the *neutral* feedback ( ) was similar to that indicating the *loss* feedback ( ), and the shape indicating the *gain* feedback ( ) was different from that indicating *neutral* or *loss* feedback. In the G sets, the shape indicating the *neutral* feedback ( ) was similar to that indicating the *gain* feedback ( ), and the shape indicating the *loss* feedback ( ) was different from that indicating the *gain* or *neutral* feedback. Participants completed three replicates of the three set types, with 120 trials in each replicate. The three D sets were always presented first, followed by the three G sets or the three L sets. The sequence of the three G set replicates and the three L set replicates were counterbalanced among the participants. Each set replicate started with 50 cents as the initial allotment, and for each trial they won or lost five or zero cent(s). For each set replicate, participants won or lost a small amount of money (e.g., 0 to 85 cents), but overall there were equal numbers of *gain*, *neutral* and *loss* feedback and each participant received a six dollar bonus at the end of the experiment.

Set Type	Reward Valence	Feedback Stimuli
D	Gain	
	Neutral	
	Loss	
L	Gain	
	Neutral	
	Loss	
G	Gain	
	Neutral	
	Loss	

Table 3.1. Experiment 4 example of the feedback stimuli.

Electrophysiological Methods

The electrophysiological methods used in Experiment 4 were very similar to those used in Experiment 1. All recording and analysis parameters were the same with one exception: twenty-two (rather than twenty-six) scalp electrodes were used, positioned at sites Fp1, Fp2, F7, F3, Fz, F4, F8, FC3, FCz, FC4, T7, C3, Cz, C4, T8, CPz, P7, P3, Pz, P4, P8, and Oz.

Results

Behavioral Results

As in the analyses in previous experiments, the frequency in which participants switched their response depending on the outcome of their previous choice was examined and plotted in Figure 3.2. In all the three types of sets, participants switched their response more often when their previous choice led to a *neutral* or *loss* feedback compared to when it led to a *gain* feedback (D sets: $F(1,16)=9.01$, $p<0.01$; L and G sets: $F(1,16) = 17.82$, $p=.001$), and they switched more often when the outcome was a *loss* feedback compared to when it was a *neutral* feedback (D sets: $F(1,16)=5.78$, $p<0.05$; L and G sets: $F(1,16) = 8.46$, $p<0.01$).

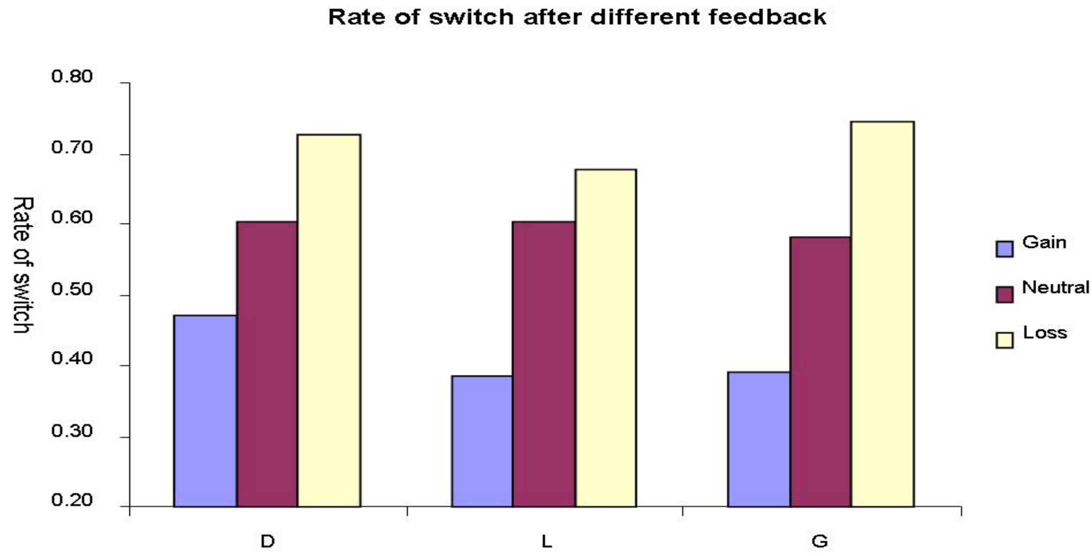


Figure 3.2. Experiment 3 behavioral results. In D sets(left), gain, neutral and loss information were indicated by three different shapes; in L sets(middle), neutral is more similar to loss than to gain; in G sets(right), neutral is more similar to gain than to loss.

Electrophysiological Results

The FRN

Consistent with Experiment 2 and 3, the FRN mean amplitude between 200 ms and 300 ms following the feedback was measured at FCz (see Figure 3.3).

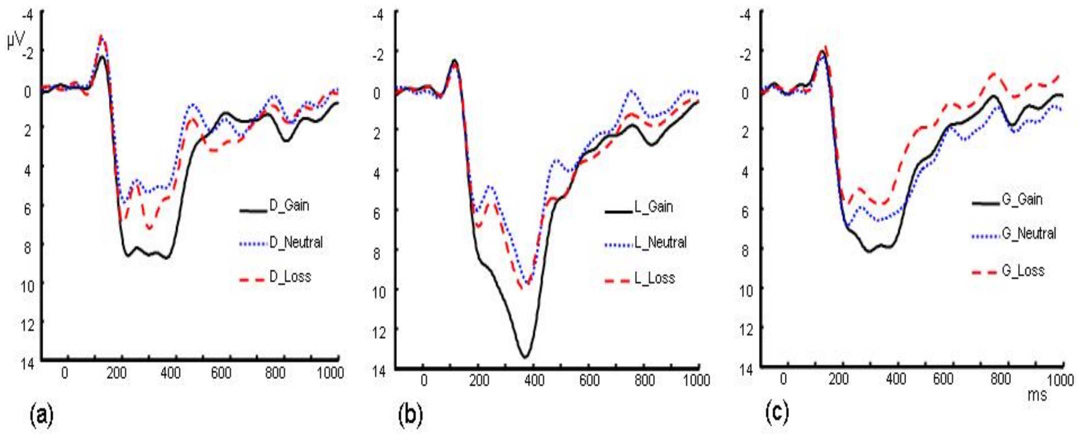


Figure 3.3. Experiment 4 ERP waveforms at electrode FCz. (a) D sets; (b) L sets; (c) G sets.

A 3×3 two-way repeated-measures ANOVA with factors *set type* and *reward valence* revealed a main effect in reward valence ($F(2, 32) = 14.31$, $p < 0.01$) and an interaction between set type and reward valence ($F(4, 46) = 3.1$, $p < 0.05$). Neutral and loss feedback elicited a larger FRN than gain feedback ($F(1, 16) = 20.7$, $p < .001$), and there was no difference between neutral and loss feedback ($F < 1$). Two repeated-measures ANOVAs were separately performed on D vs. L set type by reward valence and on D vs. G set type by reward valence. The interaction between the two factors was not significant for set type (D vs. L) and reward valence ($F < 1$), suggesting that the FRN reward valence effect was similar between D and L sets. However the interaction was significant for set type (D vs. G) and reward valence ($F(2, 32) = 5.39$, $p < 0.05$). Neutral feedback in G sets had a smaller FRN effect than in D sets ($F(1, 16) = 17.43$, $p < .001$), suggesting that the similarity between neutral and gain feedback modulated the FRN activity of the neutral feedback in G sets.

The P300

The P300 amplitude was measured as the mean amplitude between 250 ms and 350 ms at Pz (see Figure 3.4).

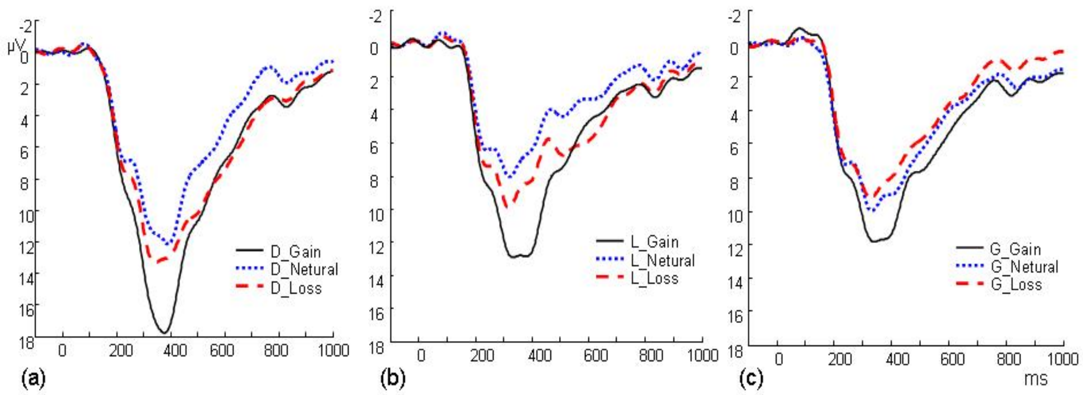


Figure 3.4. Experiment 4 ERP waveforms at electrode Pz. (a) D sets; (b) L sets; (c) G sets

A 3×3 two-way repeated-measures ANOVA with factors *set type* and *reward valence* revealed main effects in set type ($F(2, 32) = 13.26$, $p < .001$) and reward valence ($F(2, 32) = 30.76$, $p < 0.001$), in addition to an interaction between set type and reward valence ($F(4, 64) = 3.67$, $p < 0.05$). Overall D sets had a larger P300 activity than L and G sets ($F(1, 16) = 19.19$, $p < 0.001$), and there was no difference between L and G sets ($F < 1$). *Gain* feedback elicited a larger P300 than *neutral* and *loss* feedback ($F(1, 16) = 46.31$, $p < 0.001$), and the P300 difference between *neutral* and *loss* feedback was marginally significant ($F(1, 16) = 3.32$, $p = 0.08$). As the FRN analyses, two ANOVAs were conducted separately on set type (D vs. L) by reward valence and on set type (D vs. G) by reward valence. The interaction between the two factors was not significant for set type (D vs. L) and reward valence ($F < 1$), suggesting that the P300 effect was similar between D and L sets. However the interaction was significant for set type (D vs. G) and reward valence ($F(2, 32) = 4.61$, $p < 0.05$). *Neutral* feedback in G sets had a smaller P300 effect than in D sets ($F(1, 16) = 8.53$, $p < .01$), suggesting that the similarity between *neutral* and *gain* feedback modulated the P300 activity of the *neutral* feedback in G sets.

Experiment 4 Summary

Experiment 4 results obtained by manipulating the similarity among the *gain*, *neutral* and *loss* feedback in a gambling task are summarized as follows. Behaviorally participants switch their response choice more often after *loss* feedback than after *neutral* feedback, and more often after *neutral* feedback than after *gain* feedback. In all the sets, *neutral* and *loss* feedback elicited larger FRNs than *gain* feedback. However, the evoked FRN pattern among the three types of feedback were similar between D and L sets, and different between D and G sets, suggesting that in G sets the similarity between *neutral* and *gain* feedback reduced the perceptual mismatch between the received neutral feedback and primed gain feedback and evoked a smaller FRN. P300 showed effects similar to the FRN.

Experiment 5: HBS flanker gambling task

Design and Rationale

In Experiment 5, a flanker gambling task was used to investigate how the FRN elicited by the neutral target may be modulated by the presence of gain or loss flanker information along with the neutral target feedback.

In the flanker gambling task, three letters were designated to respectively indicate *gain*, *neutral* and *loss* reward information. As in Experiment 1, the feedback stimulus consisted of five letters, and only the central letter conveyed the reward information. There were nine types of flanker string: Tgain_Fgain, in which the central letter indicated *gain* feedback, and the flanker letters were identical to the central letter, e.g., HHHHH; Tgain_Fneut, in which the central letter indicated *gain* feedback, and the flanker letters indicated *neutral* feedback; Tgain_Floss, in which the central letter indicated *gain* feedback, and the flanker letters indicated loss feedback; Tneut_Fgain, in which the central letter indicated *neutral* feedback, and the flanker letters indicated *gain* feedback; Tneut_Fneut, in which the central letter indicated *neutral* feedback, and the flanker letters were identical to the central letter; Tneut_Floss, in which the central letter indicated a neutral feedback, and the flanker letters indicated loss feedback; Tloss_Fgain, in which the central letter indicated *loss* feedback, and the flanker letters indicated *gain* feedback; Tloss_Fneut, in which the central letter indicated *loss* feedback, and the flanker letters indicate *neutral* feedback; Tloss_Floss, in which the central letter indicated *loss* feedback, and the flanker letters indicate *loss* feedback. Among the nine types of feedback, Tgain_Fgain, Tneut_Fneut and Tloss_Floss were congruent feedback, and Tgain_Fneut, Tgain_Floss, Tneut_Fgain, Tneut_Floss, Tloss_Fgain, Tloss_Fneut were incongruent feedback.

It was predicted that congruent *neutral* and *loss* feedback would elicit larger FRNs than congruent *gain* feedback, and there would be no difference between congruent *neutral* and *loss* feedback. In general, incongruent feedback would elicit a larger FRN than congruent feedback. Particularly, in the gain condition, there would not be much difference between Tgain_Tneut and Tgain_Floss; in the neutral condition, Tneut_Floss may have a larger FRN than Tneut_Fgain because the appearance of gain-related features in the flanker letters may modulate the FRN amplitude evoked by the perceptual mismatch between the central neutral target and the prepared gain-related feature in the sensory system; for the same reason, in the loss condition Tloss_Fneut may have a larger FRN than Tloss_Fgain.

Methods

Participants

There were twelve participants (three males and nine females) aged between 18 and 23. All were right-handed, had normal or corrected-to-normal vision, and normal color vision. Prior to the test, participants provided written informed consent in accordance with the Institutional Review Board of the University of Michigan. They received a monetary payment for their participation.

Procedure

The procedure in Experiment 5 was similar to that in Experiment 1 with the following exceptions. There were three doors of different colors (red, blue and green) rather than four red doors apposed on the screen. The participants chose one door using their right index finger by pushing a button corresponding to the location of the chosen door. One thousand milliseconds after their choice, one of the three types of the reward information—*gain*, *neutral* and *loss*—would appear. For the gain or loss feedback, the participant won or lost 25 cents on the trial; for the neutral feedback, the participants did not win or lose any money on the trial. The three doors' position (left, middle or right) was randomly assigned during each trial. At the beginning of the experiment, H and S were assigned to indicate *gain* or *loss* feedback (the assignment was counterbalanced among the participants) and B always indicate a *neutral* feedback. There were nine types of feedback stimuli which are shown in Table 3.2. Participants completed ten sets of experimental material, with 90 trials in each set. Each set started with 50 cents as the initial allotment and participants were given summary information about the bonus they had earned every ten trials. The feedback was randomly chosen from a set of equal numbers of each type of feedback stimuli listed in Table 3.2. On average, there were roughly equal numbers of gain, neutral and loss feedback. The ratio of congruent to incongruent trials was 1:2.

Reward Valence	**Flanker types**	**Congruency**	**Type name**	**Feedback Stimuli**
Gain	Gain	Congruent	Tgain_Fgain	HHHHH
Gain	Neutral	Incongruent	Tgain_Fneut	BBHBB
Gain	Loss	Incongruent	Tgain_Floss	SSHSS
Neutral	Gain	Congruent	Tneut_Fgain	HHBHH
Neutral	Neutral	Incongruent	Tneut_Fneut	BBBBB
Neutral	Loss	Incongruent	Tneut_Floss	SSBSS
Loss	Gain	Congruent	Tloss_Fgain	HHSHH
Loss	Neutral	Incongruent	Tloss_Fneut	BBSBB
Loss	Loss	Incongruent	Tloss_Floss	SSSSS

Table 3.2. Experiment 5 example of the feedback stimuli.

Electrophysiological Methods

The electrophysiological methods in Experiment 5 were identical to those in Experiment 1.

Results

The FRN

Figure 3.5 presents the ERPs for *congruent gain*, *congruent neutral* and *congruent loss* feedback at FCz; and Figure 3.6 presents the ERPs for *gain*, *neutral* and *loss* target feedback which was surrounded by *gain*, *neutral* and *loss* flanker letters at FCz.

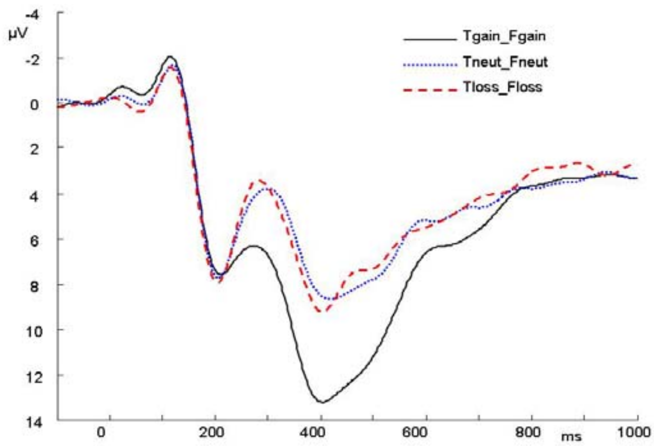


Figure 3.5. Experiment 5 ERP waveforms at FCz for congruent gain, neutral and loss feedback

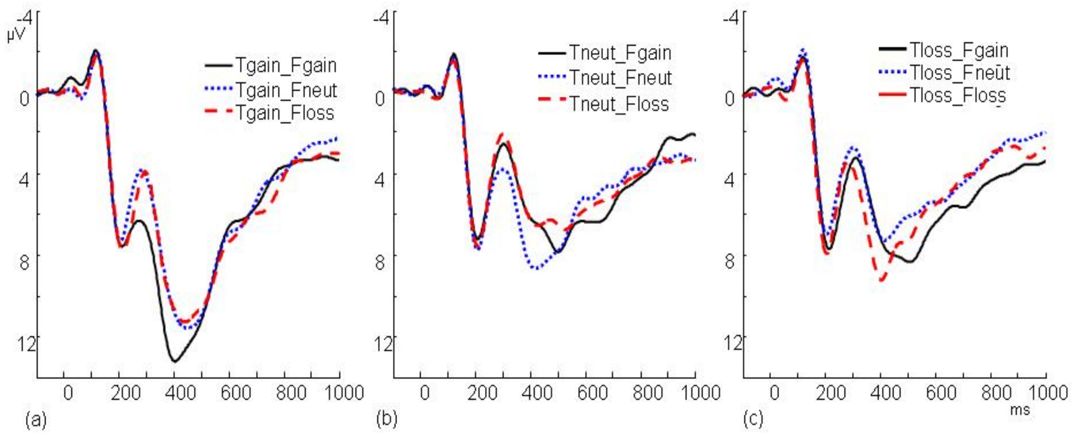


Figure 3.6. Experiment 5 ERP waveforms at FCz for (a) gain, (b) neutral and (c) loss target feedback

As Experiment 1, the FRN amplitude was measured as the mean amplitude between 250 ms and 350 ms following the feedback at FCz. A 3×3 two-way repeated-measures ANOVA with factors *target* and *flanker* revealed a main effect in target ($F (2, 22) =17.70$, $p<0.01$), a marginally significant main effect in flanker ($F (2, 22) =3.36$, $p<0.1$), and an interaction between target and flanker ($F (4, 44) =6.7$, $p<0.01$). In the congruent condition, *loss* and *neutral* feedback elicited a larger FRN than *gain* feedback ($F (1, 11) =22.22$, $p<.001$) and there was no FRN difference between congruent *neutral* and *loss* feedback ($F<1$). *Gain* target had a larger FRN when it was surrounded by *neutral* and *loss* flanker letters compared to when it was surrounded by *gain* flanker letters (F (1, 11)

= 11.57, p<0.01). There was no difference between *gain* target surrounded by *neutral* and that surrounded by *loss* flanker letters (F<1). *Neutral* target had a larger FRN when it was surrounded by *gain* and *loss* flanker letters, compared to when it was surrounded by *neutral* flanker letters (F (1, 11) = 10.09, p<0.01). There was no difference between *neutral* target surrounded by *gain* and that surrounded by *loss* flanker letters (F<1). When the target was a *loss* feedback, there was no FRN difference among the three types of flankers (F (2, 22) =2.40, p>0.1).

The baseline-to-peak measurement was also conducted: the peak amplitude of the FRN was defined as the most negative value between 200 ms and 400 ms after the onset of the feedback, and the peak latency was defined as the time when the most negative peak occurred. The FRN peak amplitude analyses revealed the same results as the FRN mean amplitude analyses. A 3×3 two-way repeated-measures ANOVA on the FRN peak latency with factors *target* and *flanker* revealed a main effect of target (F (2, 22) =4.30, p<0.05) and an interaction between target and flanker (F (4, 44) =4.55, p<0.01). In the *loss* condition, Tloss_Floss elicited an earlier FRN than Tloss_Fgain and Tloss_Fneut (F (1, 11) =9.59, p<0.05); Tloss_Fneut tended to have an earlier FRN than TLoss_Fgain (F (1, 11) =3.29, p=0.097). There was no latency difference among different flankers in *gain* or *neutral* target conditions.

It was hypothesized that *neutral* target letter may elicit a smaller FRN when it was surrounded by *gain* flanker letters, compared to when it was surrounded by *loss* flanker letters. However that difference was not observed as described above. In the experiment design, letters indicating *gain* and *loss* feedback were counterbalanced across the participants. For half of the participants, H indicated a *gain* feedback and S indicated a *loss* feedback, thus HHBHH and SSBSS respectively indicated Tneut_Fgain and Tneut_Floss. For the other half of the participants, S indicated a *gain* feedback and H indicated a *loss* feedback, thus SSBSS and HHBHH respectively indicated Tneut_Fgain and Tneut_Floss. B was chosen to be similar to H as to S. However, B may be more similar to one letter than to the other letter. If so, the external perceptual mismatch between the target and flanker letters became a confounding factor when comparing Tneut_Fgain and Tneut_Floss. To investigate this issue, in the following analysis, group information was added as a factor to test whether the specific letter assignment may cause some unexpected effect.The initial analyses were focused on how flanker letters may affect the processing of the *neutral* target letter. A 2×3 two-way repeated-measures ANOVA with factors *group* and *flanker type* was conducted on *neutral* feedback trials, and revealed a main effect of flanker ($F(2, 20) = 5.79$, $p<0.05$) and an interaction between flanker and group ($F(2, 20) = 6.90$, $p<0.05$). In Group 1 where H indicated a *gain* and S indicated a *loss*, Tneut_Fgain feedback appeared to have a larger FRN than Tneut_Fneut and Tneut_Floss feedback ($F(1, 10) = 3.50$, $p<.1$; see Figure 3.7). In contrast, in Group 2 where H indicated a *loss* and S indicated a *gain*, Tneut_Floss feedback had a larger FRN than Tneut_Fgain and Tneut_ Fneut feedback ($F(1, 10) = 42.33$, $p<0.01$).

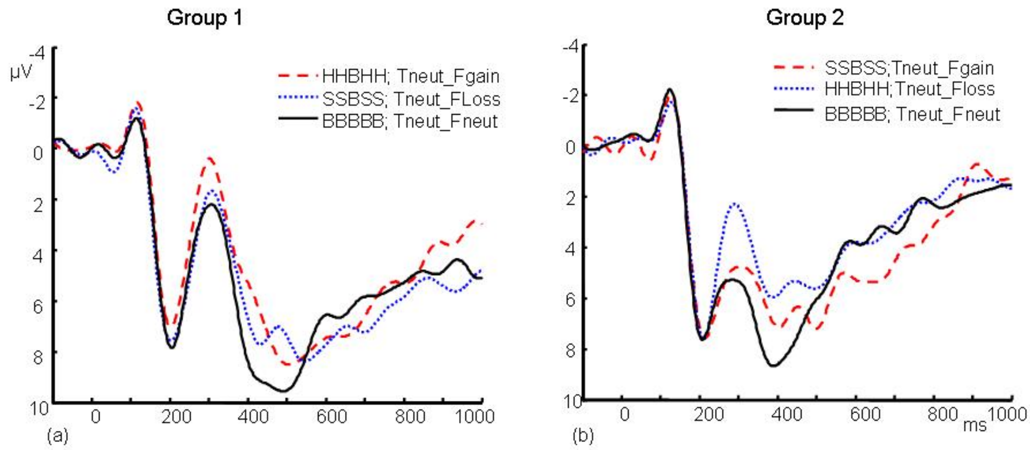


Figure 3.7. Experiment 5 ERP waveforms of neutral feedback at FCz displayed by groups.

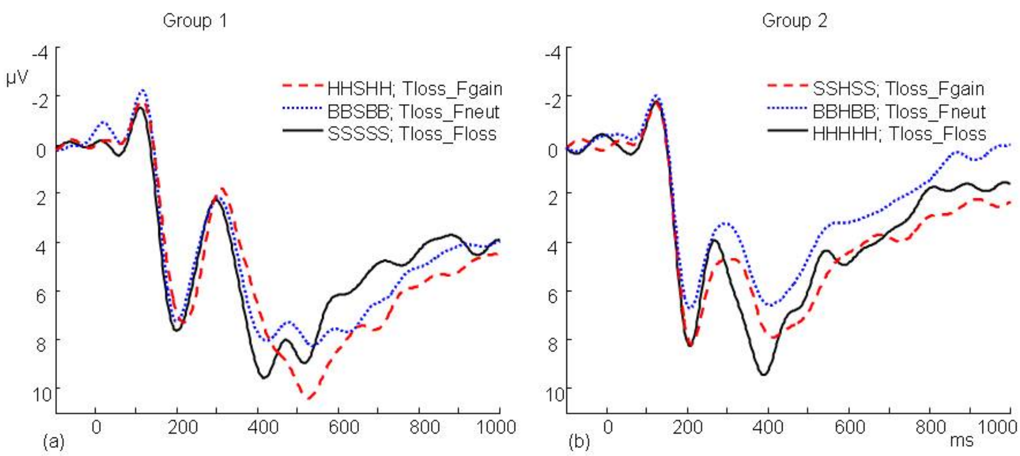


Figure 3.8. Experiment 5 ERP waveforms of loss feedback at FCz displayed by groups.

A similar group analysis was done in *loss* feedback. As shown in Figure 3.8, in Group 1, there was no difference among the three types of flanker letters (p>0.10). However in Group 2, Tloss_Fneut feedback had a larger FRN than Tloss_Fgain and Tloss_Floss feedback (F (1, 10) =5.47, p<0.05), and there was no difference between Tloss_Fgain and Tloss_Floss (F<1). Such group-related effect difference was not evident in the *gain* feedback condition.

The P300

The P300 was measured as the mean amplitude between 350 ms and 600 ms (see Figure 3.8).

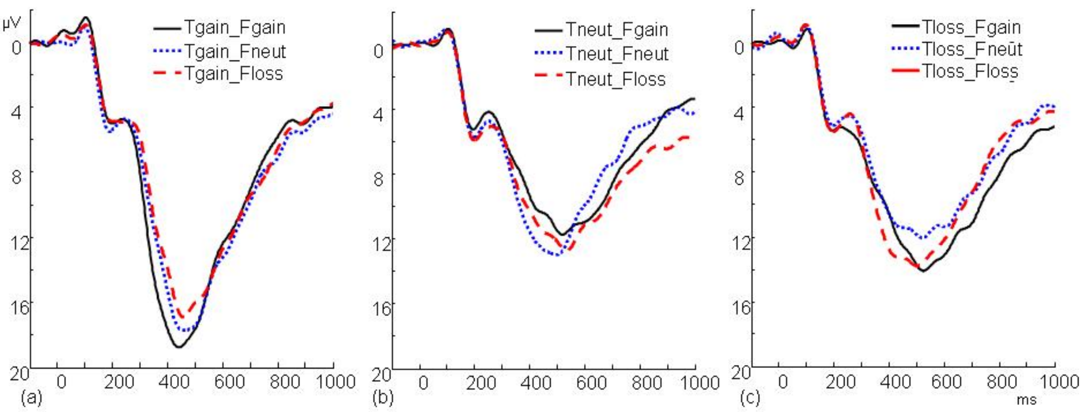


Figure 3.9. Experiment 5 ERP waveforms at Pz for (a) gain, (b) neutral and (c) loss target

A 3×3 two-way repeated-measures ANOVA with factors *target and flanker* type revealed a main effect in target type (F (2, 22) =29.04, p<.001). There was no main effect or interaction related to flanker type (main effect, F<1; interaction, F (4, 44) =2.54, p>0.10). *Gain* feedback had a larger P300 than *loss* and *neutral* feedback, and there was no difference between *loss* and *neutral* feedback.

The P300 baseline-to-peak amplitude and the peak latency were measured between 300 ms and 650 ms after the onset of the feedback. Statistics on the peak amplitude revealed the same effects as those on the above P300 mean amplitude analyses. For the peak latency analyses, a 3×3 two-way repeated-measures ANOVA with factors *target and* *flanker type* revealed a marginally significant target effect (F (2, 22) =3.12, p<0.1), and a marginally significant interaction between target and flanker (F (4, 44) =2.54, p<0.1). Post-hoc Newman-Keuls analyses showed that *gain* feedback tended to elicit an earlier P300 than *neutral* and *loss* feedback (p<0.1).

Experiment 5 Summary

Experiment 5 results obtained by using three letters indicating *gain*, *neutral* and *loss* feedback in a flanker gambling task are summarized as follows. As in Experiment 4, *neutral* and *loss* feedback elicited larger FRNs than *gain* feedback in the congruent condition, and there was no difference between congruent *neutral* and *loss* feedback. When the target was a *gain* or *neutral* feedback, *incongruent* letters (i.e., target and flanker letters were different) elicited a larger FRN than did the *congruent* letters (i.e, target and flanker letters were same) overall. This congruency effect of the FRN amplitude did not appear for the *loss* targets. However, incongruent *loss* feedback elicited a later FRN than congruent *loss* letters.

As predicted, in the incongruent gain condition, there was no difference between Tgain_Fneut and Tgain_Floss. In the incongruent neutral and loss conditions, the predicted reduced FRN when the *neutral* or *loss* target was surrounded by gain flankers was only observed in a subset of the participants. From the *neutral* feedback, it looks like the particular letter combination HHBHH elicited a larger FRN than the other neutral incongruent letter combination SSBSS regardless of the reward meaning the flanker letters carried. One possible interpretation is that the external perceptual mismatch in the letter string HHBHH is larger than in the letter string SSBSS, leading to a larger FRN congruency effect in the *neutral* feedback condition. No similar patterns were observed that would account for the results for the loss feedback condition.

Consistent with previous experiments, *gain* feedback elicited a larger P300 than *loss* feedback, and there was no P300 difference between *neutral* and *loss* feedback.

Experiment 6: HKCS gambling task

Design and Rationale

In the previous experiments where the flanker gambling task was used, incongruent feedback usually elicited a larger FRN than congruent feedback. It was hypothesized that the perceptual mismatch existing in the external feedback stimuli contributed to this FRN congruency effect; however the semantic mismatch between the target (e.g., indicating gain information) and the flanker (e.g., indicating loss information) was a confounding factor in previous experiments. In Experiment 6, two letters were designated to indicate *neutral* feedback, thereby creating an incongruent condition where target and flanker letters were perceptually different but indicated the same reward information. If the perceptual mismatch played a role in the elicitation of an incongruent FRN, a *neutral* target letter surrounded by a different *neutral* target would elicit a larger FRN compared to a *neutral* target letter surrounded by the same *neutral* target.

Methods

Participants

There were twelve participants (five males and seven females) aged between 18 and 23. All were right-handed, had normal or corrected-to-normal vision, and normal color vision. Prior to the test, participants provided written informed consent in accordance with the Institutional Review Board of the University of Michigan. They received a monetary payment for their participation.

Procedure

The procedure in Experiment 6 was similar to that in Experiment 5 with the following exceptions. The neutral feedback was indicated by two letters (i.e., C and K) rather than one letter (i.e., B). Participants completed ten sets of experimental material, with 110 (rather than 90) trials in each set. The feedback was randomly chosen from a set of feedback stimuli according to the probability listed in column 2 of Table 3.3. On average, there were roughly equal numbers of gain, neutral and loss feedback.

Reward Valence	**Probability**	**Flanker types**	**Congruency**	**Type name**	**Feedback Stimuli**
Gain	1/9	Gain	Congruent	Tgain_Fgain	HHHHH
Gain	1/18	Neutral	Incongruent	Tgain_Fneut1	KKHKK
Gain	1/18	Neutral	Incongruent	Tgain_Fneut2	CCHCC
Gain	1/9	Loss	Incongruent	Tgain_Floss	SSHSS
Neutral	1/18	Gain	Incongruent	Tneut1_Fgain	HHKHH
Neutral	1/36	Neutral	Congruent	Tneut1_Fneut1	KKKKK
Neutral	1/36	Neutral	Incongruent	Tneut1_Fneut2	CCKCC
Neutral	1/18	Loss	Incongruent	Tneut1_Floss	SSKSS
Neutral	1/18	Gain	Incongruent	Tneut2_Fgain	HHCHH
Neutral	1/36	Neutral	Incongruent	Tneut2_Fneut1	KKCKK
Neutral	1/36	Neutral	Congruent	Tneut2_Fneut2	CCCCC
Neutral	1/18	Loss	Incongruent	Tneut2_Floss	SSCSS
Loss	1/9	Gain	Incongruent	Tloss_Fgain	HHSHH
Loss	1/18	Neutral	Incongruent	Tloss_Fneut1	KKSKK
Loss	1/18	Neutral	Incongruent	Tloss_Fneut2	CCSCC
Loss	1/9	Loss	Congruent	Tloss_Floss	SSSSS

Table 3.3. Experiment 6 example of the feedback stimuli.

Electrophysiological Methods

The electrophysiological methods in Experiment 6 were identical to those in Experiment 1.

Results

There were sixteen types of feedback stimuli which were of three different probabilities. In the following analyses, comparisons were conducted among the trials which were of the same probability information. Consistent with previous experiments, the FRN amplitude was measured as the mean amplitude between 250 ms and 350 ms following the feedback at FCz

The FRN

Figure 3.10 presents the ERPs for Tgain_Fgain, Tgain_Floss, Tloss_Floss and Tloss_Fgain feedback at FCz. These four types of feedback were of the same probability around 1/9. The FRN amplitude was measured as the mean amplitude between 280 ms and 380 ms following the feedback at FCz. A 2×2 two-way repeated-measures ANOVA with factors *reward valence* and *congruency* revealed main effects in reward valence ($F(1, 11) = 30.18$, $p < 0.001$) and congruency ($F(1, 11) = 17.85$, $p < 0.01$). There was no interaction between the two factors. *Loss* feedback elicited a larger FRN than *gain* feedback. *Incongruent* feedback elicited a larger FRN than *congruent* feedback.

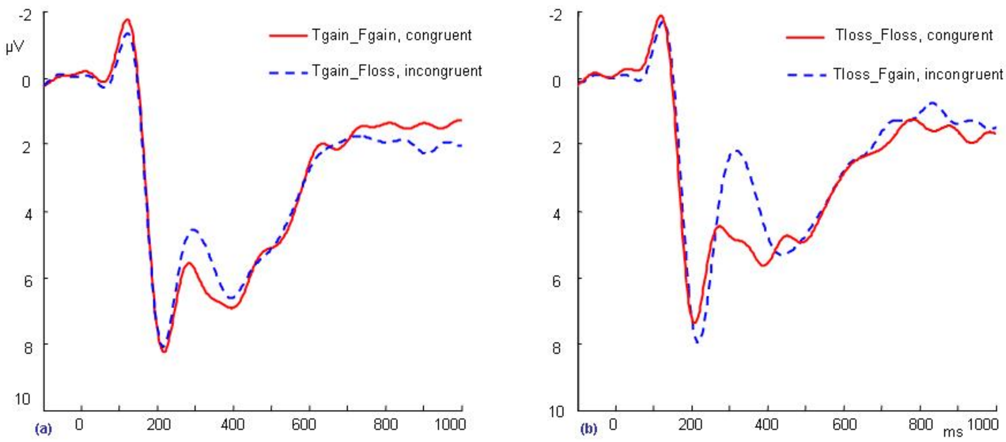


Figure 3.10. Experiment 6 ERP waveforms at FCz for (a) gain and (b) loss target feedback

The baseline-to-peak measurement was also conducted: the peak amplitude of the FRN was defined as the most negative value between 200 ms and 400 ms after the onset of the feedback, and the peak latency was defined as the time when the most negative peak occurred. The FRN peak amplitude analyses revealed the same results as the FRN mean amplitude analyses. A 2×2 two-way repeated-measures ANOVA on the FRN peak latency with factors *reward valence* and *congruency* revealed a main effect in congruency ($F(1, 11) = 8.57$, $p < 0.05$). Incongruent feedback elicited a later FRN than congruent feedback. There was no main effect in reward valence or interaction between the two factors ($F < 1$).

Figure 3.11 presents the ERPs for congruent *neutral* (including both Tneut1_Fneut1 and Tneut2_Fneut2) and incongruent *neutral* feedback (including Tneut1_Fneut2 and Tneut2_Fneut1) at FCz. Incongruent *neutral* feedback elicited a larger FRN than congruent *neutral* feedback for both the FRN peak and mean amplitude (peak, $F(1,11)=13.41$, $p<0.01$; mean, $F(1,11)=7.87$, $p<0.05$). Incongruent *neutral* feedback tended to have a later FRN peak than congruent *neutral* feedback ($F(1, 11)=4.39$, $p=0.06$).

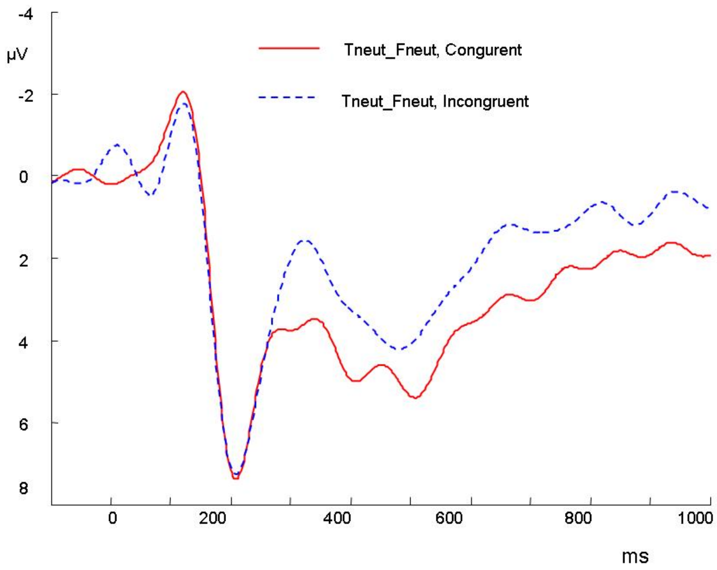


Figure 3.11. Experiment 6 ERP waveforms at FCz for congruent (e.g., CCCCC and KKKKK) and incongruent (e.g., CCKCC and KKCKK) neutral feedback

The P300

The P300 was measured as the mean amplitude between 350 ms and 600 ms (see Figure 3.12). A 2×2 two-way repeated-measures ANOVA with factors *reward valence* and *congruency* revealed main effects in reward valence ($F(1, 11)=15.39$, $p<0.01$) and congruency ($F(1, 11)=6.83$, $p<0.05$). There was no interaction between the two factors ($F<1$). *Gain* feedback had a larger P300 than *loss* feedback. *Congruent* feedback elicited a larger P300 than *incongruent* feedback.

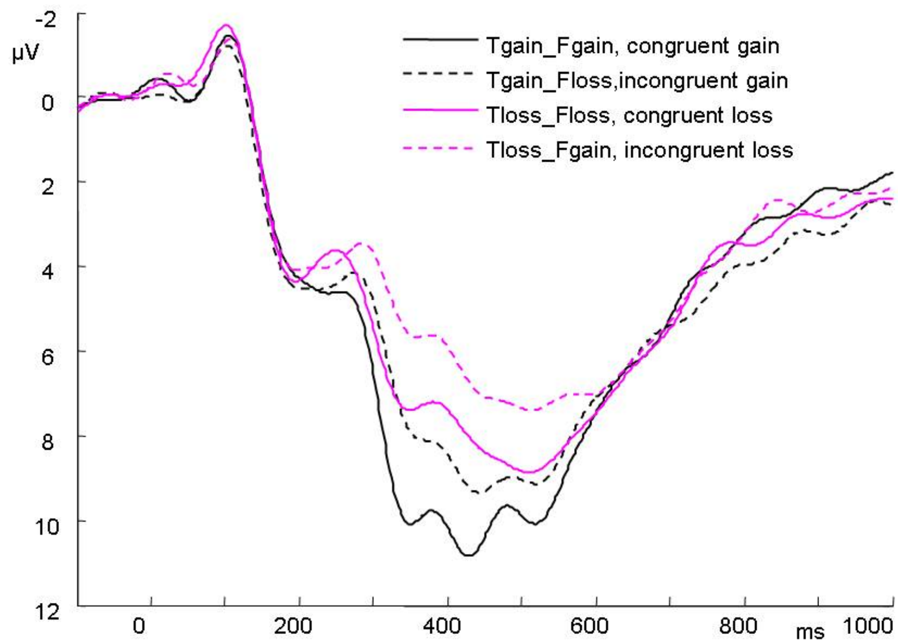


Figure 3.12. Experiment 6 ERP waveforms for congruent and incongruent gain and loss feedback at Pz

The P300 baseline-to-peak amplitude and the peak latency were measured between 300 ms and 650 ms after the onset of the feedback. Statistics on the peak amplitude revealed the same effects as those on the above P300 mean amplitude analyses. A 2×2 two-way repeated-measures ANOVA on the FRN peak latency with factors *reward valence* and *congruency* revealed marginally significant main effects in reward valence ($F (1, 11) =4.33$, $p=0.06$) and congruency ($F (1, 11) =4.53$, $p=0.057$). Incongruent feedback tended to have a delayed P300 relative to congruent feedback. *Loss* feedback tended to have a delayed P300 relative to *gain* feedback. There was no interaction between the two factors ($F<1$).

Figure 3.13 presents the ERP waveforms for congruent neutral (including both Tneut1_Fneut1 and Tneut2_Fneut2) and incongruent neutral feedback (including Tneut1_Fneut2 and Tneut2_Fneut1) at Pz. Congruent neutral feedback elicited a larger P300 than incongruent feedback for both the peak and mean amplitude (peak amplitude, $F (1, 11) =17.18$, $p<0.01$; mean amplitude, $F (1, 11) =11.00$, $p<0.01$). There was no latency difference between the two types of feedback ($F (1, 11) =2.30$, $p>0.10$).

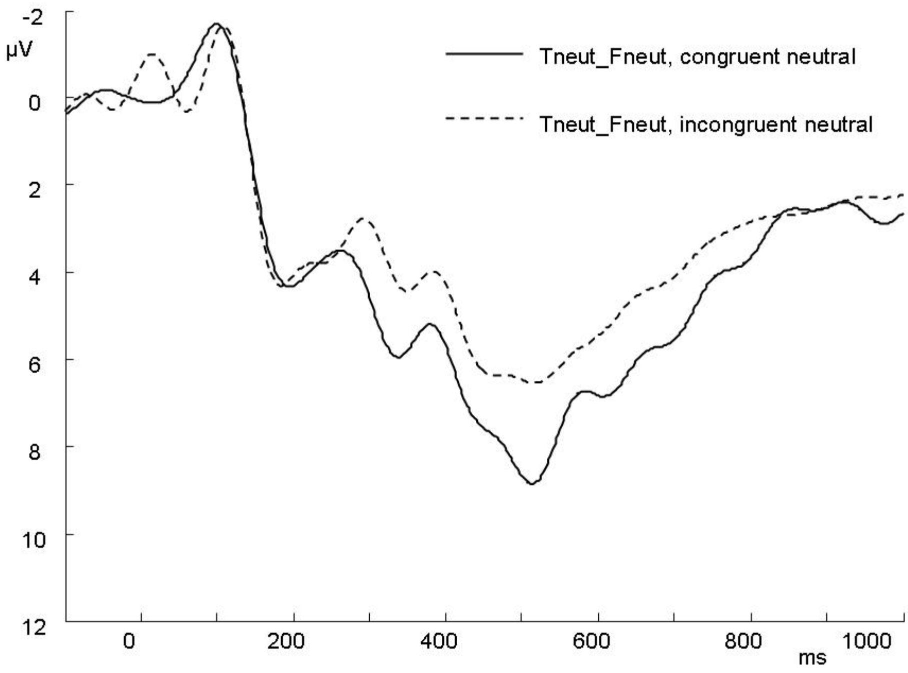


Figure 3.13. Experiment 6 ERP waveforms at Pz for congruent (e.g., CCCCC and KKKKK) and incongruent (e.g, CCKCC and KKCKK) neutral target feedback

Experiment 6 Summary

Experiment 6 results obtained by using two letters indicating *neutral* feedback in a flanker gambling task are summarized as follows. Consistent with Experiment 1 results, *loss* feedback elicited a larger FRN than *gain* feedback, and incongruent feedback elicited a larger FRN than congruent feedback. The most interesting result was that when one *neutral* target letter was surrounded by four different *neutral* flanker letters, the FRN was larger compared to when one *neutral* target letter was surrounded by four identical flanker letters, suggesting that the FRN congruency effect could not be simply explained by semantic mismatch between the target and flanker letters.

Gain feedback elicited a larger P300 than *loss* feedback; congruent feedback elicited a larger P300 than incongruent feedback in both the *gain* and *loss* reward conditions. When both the target and flanker letters indicated *neutral* feedback, congruent feedback elicited a larger P300 than incongruent feedback as well.

Chapter III Discussion

In this chapter, another three experiments were conducted to examine how the FRN elicited by the *neutral* feedback may be modulated through manipulating its perceptual similarity to *gain* and *loss* feedback or presenting interfering information along with the *neutral* target information. It was generally found that *neutral* and *loss* feedback elicited a larger FRN than *gain* feedback and there was no difference between *neutral* and *loss* feedback. However the FRN effect in response to *neutral* feedback was smaller when it was perceptually similar to the *gain* feedback compared to when it was perceptually similar to *loss* feedback or different from both the *gain* and *loss* feedback, and there was no FRN effect difference between the *neutral* feedback that was perceptually similar to *loss* feedback and the *neutral* feedback that was perceptually different from both the *loss* and *gain* feedback. These results suggested that (1) the perceptual system was tuned for gain-related rather than loss-related perceptual attributes; (2) the FRN was increased when the mismatch between the actual outcome and the gain perceptual tuning was detected regardless of the delivered feedback being a neutral or a loss feedback; (3) the amplitude of the FRN was modulated by the degree of perceptual mismatch between the actual outcome and the gain perceptual tuning in the perceptual system.

Consistent with the observation in Chapter II Experiment 1 results, the presence of incongruent flanker reward information enhanced the FRN in the gain feedback condition in Experiment 5 and 6. In the incongruent gain condition, the presence of the loss-related features in the flanker stimuli on one hand induced the internal mismatch between the actual outcome and the gain perceptual tuning, and on the other hand induced the external mismatch in the feedback stimuli. Both the internal and external mismatch led to the enhancement of the FRN as seen in all the incongruent gain conditions in the flanker gambling tasks.

For the loss feedback condition, the FRN congruency effect was very prominent in Experiment 6, but not evident in Experiment 5. In the incongruent loss condition, the loss target elicited a larger FRN because of the internal mismatch between the central loss target in the actual outcome and the gain perceptual tuning in the perceptual system.

This FRN effect, however, was reduced by the presence of the gain-related features in the flanker stimuli which reduced the internal mismatch between the actual outcome and the gain perceptual tuning in the perceptual system. The external mismatch existing in the feedback stimuli still evoked a large incongruent FRN. Thus in the incongruent loss condition, the FRN reflected the net effect of the internal mismatch induced by the loss target and gain flankers as well as the external mismatch between loss target and gain flankers. If the modulation effect induced by the presence of gain-related features in the flanker stimuli was equal to or larger than the congruency effect induced by the external mismatch between loss target and gain flankers, the FRN effect in the incongruent loss condition would be comparable to or smaller than that in the congruent loss condition. Otherwise, the external mismatch would enhance the FRN effect in the incongruent loss condition compared to the congruent loss condition.

The prominent large FRN effect observed in Experiment 6 is probably because the involvement of the various types of letter combinations demanded participants' special attention to the perceptual mismatch involved in the feedback stimulus, which led to the enhancement of the incongruent FRN. Meanwhile, the modulation effect induced by the presence of the gain-related feature may not have been very strong. Instead in Experiment 5, for some reason, the modulation effect induced by the presence of gain-related features in the flanker was larger than the congruency effect evoked by the external mismatch; thus the incongruent loss did not elicit a larger FRN than the congruent loss. Inspection of Group 2 ERP waveforms in the loss condition (see Figure 3.8 right) showed that they were similar to the ERP waveforms in the loss condition using similar letters indicating reward information in Experiment 1 (see Figure 2.2 left). In both cases, incongruent loss feedback elicited a later but not larger FRN than the congruent feedback loss. It is possible that when the target and the flanker letters were similar to each other, for example in the similar letter conditions of Experiment 1, the external mismatch may only induce a small FRN congruency effect, which was offset by the modulation effect induced by the presence of the gain-related features in the flanker stimuli. A similar explanation may be applied for the Experiment 5 results as well although details need to be figured out about the factors affecting the modulation effect and congruency effect.

For the neutral target feedback condition, the FRN congruency effect was evident on some letter combinations but not others regardless of the reward information the flanker letters indicated, suggesting that the incongruent FRN may be elicited by the perceptual mismatch in the stimulus itself rather than the semantic mismatch between the reward information the target and flanker letters respectively carried. This assertion was supported by the finding that when both the target and flanker letters indicate neutral feedback, the incongruent Tneut_Fneut feedback elicited a larger FRN than the congruent Tneut_Fneut feedback in Experiment 6.

In addition to the FRN results, it was found that behaviorally participants switch their response more often after loss feedback than after neutral feedback, and after neutral feedback than after gain feedback. Gain feedback elicited a larger P300 than neutral and loss feedback, and neutral feedback tended to elicit a P300 similar to the loss feedback.

Chapter IV Experiment 7

Experiment 7: Known vs. unknown gambling task

Design and Rationale

Experiment 7 continued to use a flanker gambling task to investigate the factors contributing to the FRN effect. In this experiment, in addition to the regular known reward trials as previous experiments in Chapter II and III, there included a small portion of trials in which the reward valence was not disclosed to the participants until the end of the experiment. Unlike the neutral feedback used for gambling tasks in Chapter III, the unknown feedback in this design was not connected to certain meaning representations. As a typical flanker-gambling feedback letter string, the reward unknown feedback consisted of five identical (congruent condition, e.g., BBBBB) or different (incongruent condition, e.g., CCBCC) letters. Participants were told that the reward information indicated by the central target letter conveyed gain or loss information, which would be disclosed to them at the end of the experiment.

By including these trials, it is possible to clarify the argument that the larger FRN congruency effect in incongruent neutral feedback (e.g., “KKCKK”) compared to congruent neutral feedback (e.g., “CCCCC”) in Experiment 6 is due to pure bottom-up perceptual mismatch or to the perceptual mismatch that has to be modulated by the top-down reward representations. If the FRN were sensitive to the bottom-up perceptual mismatch, the incongruent unknown feedback (e.g., “CCBCC”) would elicit a larger FRN than the congruent unknown feedback (e.g., “BBBBB”) because of the perceptual interference from flanker letters. However, if the FRN were sensitive to the perceptual mismatch between two reward representations, there would no FRN difference between congruent and incongruent unknown feedback since the target (e.g., “B”) and flanker letters(e.g., “C”) did not have particular representations to correspond.

Methods

Participants

There were twenty participants (six males) aged between 18 and 33. All were right-handed, had normal or corrected-to-normal vision, and normal color vision. Prior to the test, participants provided written informed consent in accordance with the Institutional Review Board of the University of Michigan. They received a monetary payment for their participation. One male participant was eliminated for data analysis due to a large slow drift that appeared in the raw EEG data.

Procedure

The participants were seated comfortably 60 cm in front of a fourteen-inch CRT computer monitor and they were instructed to remain as still as possible and to minimize eyeblinks throughout the experiment. Materials were presented using *Presentation* (Neurobehavior System). On each trial of the experiment (see Figure 4.1 for an example), the participants were presented with two squares (one red and one blue) apposed on the screen following a 500 ms central fixation, and was instructed that each one contained gain or loss information. Squares remained on the screen until the participants selected one of them by pressing a button with their left or right index finger, corresponding to the location of the chosen square. Five milliseconds after their response, the reward information indicating whether they won or lost on the trial came up and was present for 600 ms. The inter-trial interval (ISI) was 1000 ms.

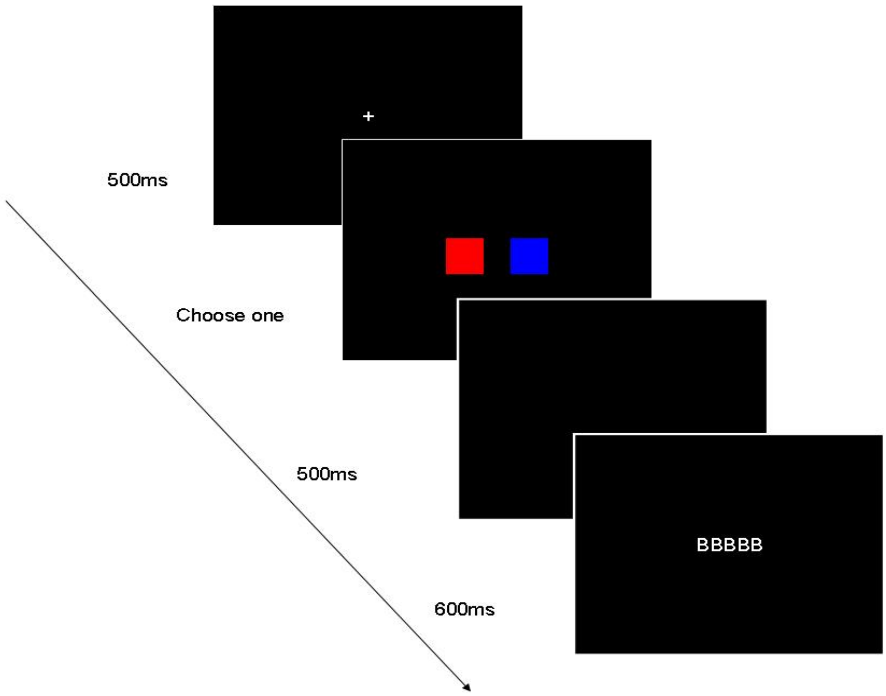


Figure 4.1. A schematic representation of Experiment 7

The reward information was a letter string in the form of the flanker stimuli— one target letter (e.g., letter D) at the center was surrounded by identical (e.g., DDDDD; *congruent* condition) or different letters (e.g., XXDXX; *incongruent* condition) and only the central letter conveyed the reward information. Four letters (i.e., D, X, S and F) were used to create the feedback stimuli. Among them the reward valence (*gain* or *loss*), indicated by two letters (e.g., D and X) were revealed to the participants at the beginning of the experiment. This type of trials took around 75% of all the trials. Participants knew whether they won or lost during the trial right after they saw the feedback letters. The reward valence indicated by the other two letters (e.g., S and F) were not disclosed to the participants until the end of experiment. This type of trials took around 25% of all the trials. Participants were not aware whether they won or lost during the trial when they saw the feedback. In this way eight letter combinations (i.e., DDDDD, XXDXX, XXXXX, DDXDD, SSSSS, FFSFF, FFFFF, SSFSS) form six experimental conditions (i.e., *congruent gain*, *congruent loss*, *incongruent gain*, *incongruent loss*, *congruent unknown*, and *incongruent unknown*) as shown in Table 4.1.

	Reward Valence	Congruency	Type name	Feedback Stimuli
Known (75%)	Gain	Congruent	Gain_con	BBBBB
	Gain	Incongruent	Gain_inc	KKBKK
	Loss	Congruent	Loss_con	KKKKK
	Loss	Incongruent	Loss_inc	BBKBB
Unknown (25%)		Congruent	Unkn_con	HHHHH OOOOO
		Incongruent	Unkn_inc	OOHOO HHOHH

Table 4.1. Experiment 7 example of the feedback stimuli.

Position (left or right) and color (red or blue) of the squares were randomly assigned for each trial. Feedback letters were retrieved randomly from a population where the ratio of 3:3:3:3:1:1 was assigned to the trial-types *"congruent gain", "incongruent gain", "congruent loss", "incongruent loss", "congruent unknown" and "incongruent unknown"* respectively. The assignment of the letters indicating known information and reward information was counterbalanced among participants. There were six sets of experimental material with 160 trials in each set. Each set started with 80 points as the initial allotment. For each gain participants won five points and for each loss participants loss five points. Participants were given summary information about points they had earned on known feedback trials every 40 trials; the points received from unknown feedback trials were added to the final points at the end of the experiment. Then points were transformed into money, and on average, each participant receive a three-to-five dollar bonus.

Electrophysiological Methods

EEG was collected using a 64-channel Active Two Biosemi system (BioSemi, Amsterdam). Eye-movements were recorded with six electrodes placed on the outer canthus, supra-orbital ridge, and cheekbone of the left and right eyes. Signals were sampled at the rate of 512 points per second and digitized with a 24 bit ADC. All electrodes were re-referenced offline to averaged mastoids.

For the ERP waveforms, a 1100 ms epoch of data (100 ms baseline) was extracted from the continuous data file for analysis. EEG data were corrected for vertical and horizontal ocular movement artifacts using the algorithm described in Gratton, Coles and Donchin's paper (Gratton, Coles & Donchin, 1983). Statistical analyses were performed on the data without any additional filtering. The data presented in the figures were filtered with a nine point Chebyshev II low-pass digital filter with a half-amplitude cutoff at 12 Hz (Matlab 7.04; Mathworks, Natick, MA). For all analyses, *p* values if all main and interaction effects were corrected using the Greenhouse-Geisser method for violations of the sphericity assumption in repeated-measures effects.

Results

The grand average waveforms were plotted at the midline scalp electrodes (see Figure 4.2). An inspection of waveforms revealed a negative ERP component enhanced between 200 ms and 400 ms for loss feedback as well as incongruent feedback at the frontal electrodes, and a positive ERP component enhanced between 300 ms and 500 ms for loss feedback at the centroparietal electrodes. The early negative component corresponds to the FRN, and its amplitude and latency was evaluated at the FCz where the negative peak was the most prominent. The later positive waveform corresponds to the P300, and its amplitude and latency were evaluated at the Pz where the positive peak reached the maximum.

The FRN

The FRN amplitude and latency were measured peak-to-peak according to the following criterion. *First*, the most positive value of the ERP waveforms was identified within a 160-240 ms window following the onset of the feedback stimuli. *Then,* the most negative value of the ERP waveforms was identified within a 240-380 ms window. The amplitude of the negativity was defined as the difference between the most negative value retrieved from the 240-380 ms window and the most positive value retrieved from the 160-240 ms window. The latency of the negativity was defined as the time when the most negative value peaked within the 240-380 ms window.

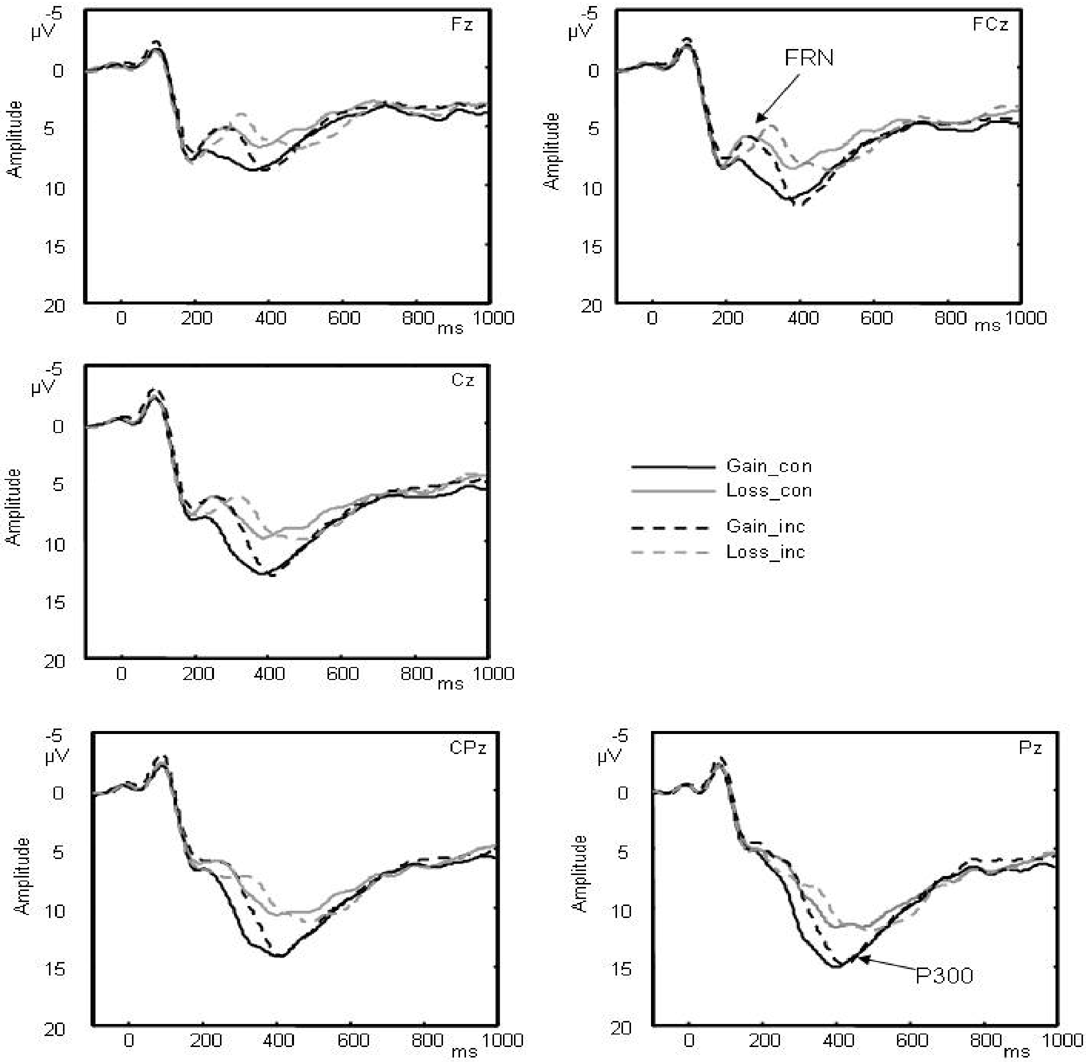


Figure 4.2. Experiment 7 ERP waveforms at midline electrodes.

Known feedback

A 2×2 two-way repeated-measures ANOVA with factors *reward valence and congruency* was conducted on both the FRN amplitude and latency. For the amplitude analysis, the main effects in both the reward valence and the congruency factors were significant (*gain* vs. *loss*, F (1, 18) = 17.36, *p*< 0.01; congruent vs. incongruent, F (1, 18) = 7.7, *p*< 0.05). *Loss* feedback elicited a larger FRN than *gain* feedback; *incongruent* feedback elicited a larger FRN than *congruent* feedback. The interaction between the two factors was not significant (F<1). For the latency analysis, again the main effects in both the reward valence and the congruency factors were significant (*gain* vs. *loss*, F (1, 18) = 9.17, *p*< 0.01; *congruent* vs. *incongruent*, F (1, 18) = 7.4, *p*< 0.05). The peak latency of the FRN elicited by *loss* feedback was later than *gain* feedback; and the peak latency of the FRN elicited by *incongruent* feedback was later than *congruent* feedback. There was no interaction between the reward valence and the congruency on the peak latency of the FRN (F<1).

Unknown feedback

No FRN amplitude or latency peak difference was found between congruent and incongruent unknown feedback (amplitude, t=.41, p>0.1; peak latency, t =.42, p>0.1).

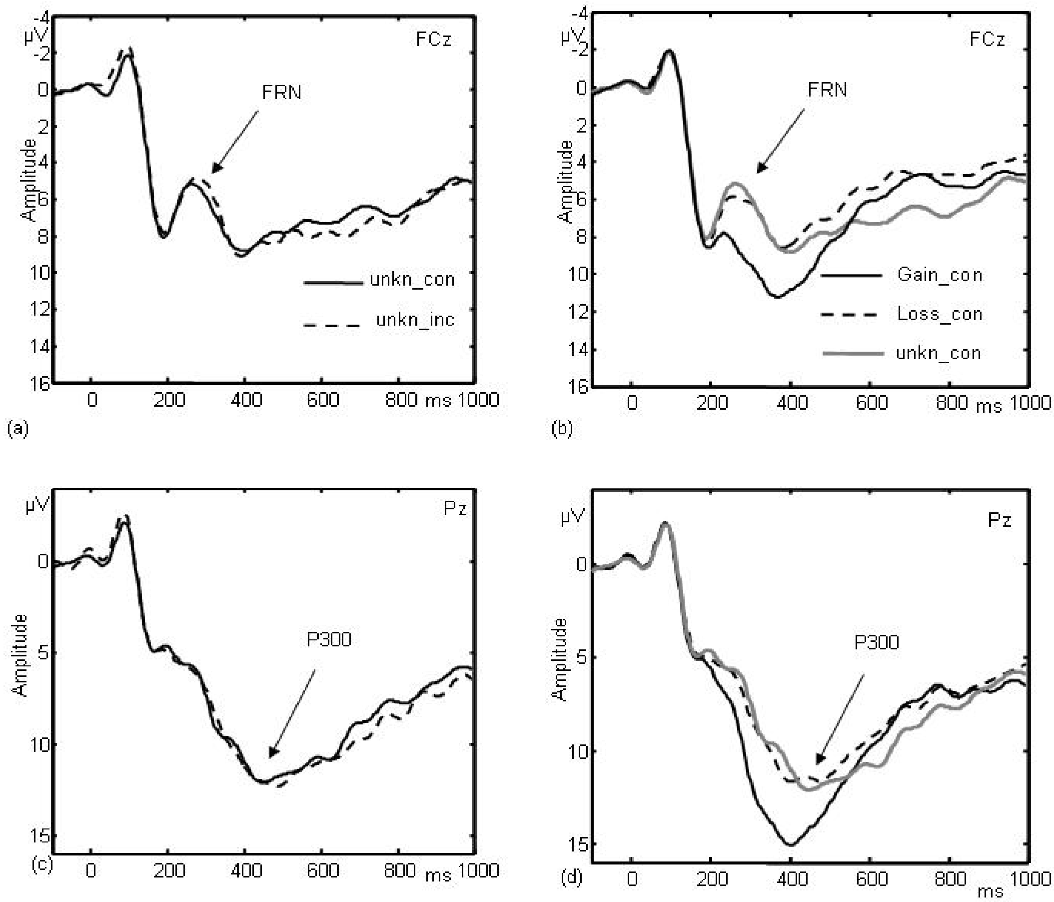


Figure 4.3. Experiment 7 congruent ERP waveforms at known vs. unknown conditions at midline electrodes.

Known vs. Unknown feedback

The knowing effect was evaluated only at the congruent feedback condition since congruent and incongruent unknown feedbacks have comparable FRN. A one-way ANOVA with factor congruent feedback type (*congruent gain, congruent loss* and *congruent unknown*) was conducted for both the FRN amplitude and peak latency. The FRN amplitude analysis revealed a main effect in feedback type ($F(2, 36) = 15.08$, $p<0.01$). Post-hoc Newman-Keuls tests showed that both *congruent loss* and *congruent unknown* feedback elicited a larger FRN than *congruent gain* feedback ($p<0.01$), and there was no difference between *congruent loss* and *congruent unknown* feedback ($p>0.1$). The FRN peak latency difference was only marginally significant among the three types of congruent feedback ($F(2, 36) = 3.14$, $p=.06$).

The P300

The P300 amplitude was measured as the most positive value of the ERP waveforms between 300 ms and 600 ms following the onset of the feedback stimuli; and the P300 peak latency was defined as the time when the most positive peak occurred.

Known feedback

A 2×2 two-way repeated-measures ANOVA with factors *reward valence and congruency* was conducted on both the P300 amplitude and peak latency. The analysis on the P300 amplitude revealed a main effect in reward information ($F(1, 18) = 20.63$, $p<0.01$). *Gain* feedback elicited a larger P300 than *loss* feedback. There was no main effect in congruency ($F<1$) or interaction between reward valence and congruency factors ($F(1, 18) = 2.50$, $p>.1$). For the latency analysis, the main effects in both the reward valence and congruency factors were significant (reward valence, $F(1, 18) = 19.08$, $p<0.01$; congruency, $F(1, 18) = 5.21$, $p<0.05$). *Gain* feedback had an earlier P300 than *loss* feedback, and *congruent* feedback had an earlier P300 than *incongruent* feedback. No interaction was found between these two factors ($F(1, 18) = 2.36$, $p>.1$).

Unknown feedback

There was no FRN amplitude ($t = .09$, $p>0.1$) or latency difference ($t = .07$, $p>0.1$) between congruent and incongruent uncertain feedback.

Known vs. Unknown feedback

As the FRN analysis, the knowing effect was evaluated only at the congruent feedback stimuli. One-way ANOVA with feedback types (*congruent gain, congruent loss* and *congruent unknown feedback*) as factor was conducted on both the P300 amplitude and peak latency. The P300 amplitude analysis revealed a significant difference among the three types of congruent feedback ($F(2, 36) = 14.43$, $p<0.01$). Post-hoc Newman-Keuls tests showed *that congruent gain* feedback had a larger P300 amplitude than *congruent loss* ($p<0.01$) and *congruent unknown* ($p<0.01$) feedback, and there was no difference between *congruent loss* and *congruent unknown* feedback ($p>0.1$). For the peak latency analysis, a significant difference was found among the three types of congruent feedback ($F(2, 36) = 3.67$, $p<0.05$). Post-hoc Newman-Keuls tests showed that *congruent unknown* feedback had a delayed P300 peak latency compared to *congruent gain* ($p<0.05$), and there was no such difference between *congruent unknown* and *congruent loss* feedback ($p>0.10$).

Experiment 7 Summary

The results obtained by manipulating the reward valence, congruency and participants' knowledge of the feedback stimuli in a flanker gambling task are summarized as follows. Consistent with previous research, in the known reward information condition, *loss* feedback elicited a larger FRN than *gain* feedback, and incongruent feedback elicited a larger FRN than congruent feedback in both the *gain* and *loss* feedback. Furthermore, congruent unknown feedback elicited a larger FRN than congruent gain feedback and its FRN amplitude was comparable to that of the congruent loss feedback condition. The most striking result is that there was no FRN difference between the congruent and incongruent unknown feedback.

Consistent with previous experiments in this study, the P300 was larger in the *gain* feedback condition than in the *loss* feedback condition. However, different from previous research, no P300 difference was found between congruent and incongruent feedback conditions. In addition, the P300 in the unknown feedback conditions was comparable to that in the loss feedback condition.

Chapter IV Discussion

In this chapter, one experiment was conducted to explore the nature of the perceptual mismatch that elicited the FRN. Consistent with previous experiments in this study, it was observed that *loss* feedback elicited a larger FRN than *gain* feedback, and incongruent feedback elicited a larger FRN than congruent feedback. These results suggest that both the internal and external mismatch contributed to the enhancement of the FRN. In addition, the lack of difference between unknown congruent and unknown incongruent feedback suggested that the FRN was not responsive to the bottom-up external mismatch per se. Instead the mismatch between two reward representations led to the enhancement of the FRN. Inconsistent with Experiment 1 results, there was no interaction between the reward valence and congruency in Experiment 7. However, inspection of the ERP waveforms at FCz in Experiment 7 (Figure 4.2) shows it was similar to the ERP waveforms elicited by dissimilar letter feedback in Experiment 1 (Figure 2.2, right).

Furthermore, similar to the congruent loss feedback, the unknown feedback elicited a larger FRN and a smaller P300 than the known congruent gain feedback. The FRN result was consistent with Holroyd et al. (2006)'s Experiment 2 findings in which the *neutral* feedback denoted uninformative information about whether participants won or lost during the trial, and the FRN elicited by the *neutral* feedback was comparable to that elicited by the *loss* feedback, both being larger than that elicited by the gain feedback. The enhancement of the FRN in the unknown condition may be explained by the infrequency (25% in Experiment 7, and 1/3 in Holroyd et al's Experiment 2) of the unknown feedback, since it is known that the rarer event in the oddball paradigm usually elicits a larger N2b component as reviewed in the introduction chapter. However, it is unlikely that the probability effect could explain all the ERP variations in the unknown feedback considering the evidence that (1) the FRN amplitude is hard to manipulate through changing the probability of reward information in gambling tasks (Hajcak et al, 2005a, 2007), and (2) the enhancement of the N2 to the probability information is usually coupled with the enhancement of the P300 (Squires et al., 1977; Squires et al., 1976). The reduction of the P300 amplitude in the unknown feedback cast doubts upon whether the FRN was the N2 component which is sensitive to the probability information in the classic oddball paradigms. Instead, the similarity of the ERP waveforms between the unknown feedback and the known congruent loss feedback suggests that the enhancement of the FRN in these two types of feedback may have been induced by the same underlying mechanism. For example, the unknown feedback were received and compared with the gain perceptual tuning in the perceptual system, and then an FRN was elicited upon the detection of the internal mismatch between them. To exclude the influence of the probability information, future studies should be designed to include the same number of known and unknown feedback stimuli.

The P300 results in Experiment 7 are quite interesting in that *gain* feedback elicited a larger P300 than *loss* feedback regardless of the congruency of the feedback stimuli. From this result, it may be proposed that it is the P300 rather than the FRN component that codes for reward valence information. However, a larger P300 was elicited by the incongruent feedback than congruent feedback in Experiment 1 and Experiment 6. Similar findings have been obtained in choice reaction time studies, where a reduced P300 was observed on incongruent trials (Zhou et al., 2004; Valle Inclan, 1996; Ragot, 1984; Ilan & Polich, 1999; Sebanz et al., 2006). Various proposals have been suggested: (1) the reduced P300 amplitude reflects a response selection conflict (Zhou et al., 2004; Ragot, 1984); (2) this effect is a consequence of perceptual interference (Sebanz et al., 2006); (3) this effect can be attributed to increased variability in P300 latency (Valle Inclan, 1996); or (4) this effect is caused by the overlapping of a slow wave activity occurring early in the congruent condition (Ilan & Polich, 1999). For the current experiment, given that there was no response execution following the feedback, it seems unlikely that the reduced P300 in the incongruent trials reflects response conflict, but all the other proposals are applicable. In addition, the FRN congruency effect may be carried over to the P300 latency window, leading to a reduced P300 in the incongruent trials. All types of contributing factors, interacting with particular participants and task situations led to the inconsistent P300 congruency effects among different experiments.

Chapter V General Discussion

The FRN and the perceptual mismatch hypothesis

The main results on the FRN

In this dissertation study, seven experiments were conducted to investigate how the feedback-related negativity may be affected by the perceptual properties of the feedback stimuli. It was found that *loss* feedback elicited a larger FRN than *gain* feedback, and this FRN reward effect was modulated by the perceptual similarity between *gain* and *loss* feedback. *Neutral* feedback elicited a larger FRN than *gain* feedback, and there was no FRN difference between *neutral* and *loss* feedback. The FRN reward effect elicited by the *neutral* feedback could be modulated by the similarity between *neutral* and *gain* feedback. When the *neutral* and *gain* feedback were similar, the FRN reward effect was smaller compared to when the *neutral* and *gain* feedback were different. Moreover, perceptually salient feedback tended to have a larger FRN effect than less perceptually salient feedback, and in particular when the reward information was indicated by conjoined features, the FRN reward effect was diminished.

The presence of the flanker reward information modulated the FRN-like negativity following the onset of the feedback stimuli. In general incongruent feedback elicited a larger FRN than congruent feedback. This FRN congruency effect was affected by the perceptual similarity between target and flanker letters—dissimilar incongruent letter strings elicited a larger FRN congruency effect than similar incongruent letter strings. When the target and the flanker letters both mapped to neutral reward, the incongruent neutral feedback elicited a larger FRN than congruent neutral feedback, suggesting that the FRN congruency effect could not be attributed to the semantic congruency between target and flanker letters. Furthermore, unknown feedback elicited a larger FRN than known congruent gain feedback. The lack of a difference in the FRN between unknown congruent and incongruent letter strings, suggests that pure bottom-up perceptual mismatch cannot explain the enhancement of the FRN in the incongruent letter string. In order to elicit an FRN incongruency effect, the perceptual mismatch has to be produced between two reward representations.

The perceptual mismatch hypothesis

As discussed in the introduction chapter, the original RL-ERN assumes that the monitoring system in the basal ganglia learns through a conditioning process in which ongoing events predict a good or bad outcome and the FRN is linearly related to the objective value of those events (Holroyd & Coles, 2002; Nieuwenhuis et al., 2004). To explain the experimental results that the evaluation system produces the FRN in a binary rather than graded manner as reported in several studies (Yeung & Safney, 2004; Hajcak et al., 2006; Holroyd et al., 2004; Holroyd et al., 2006), a cognitive preprocessing system was added to the model before the monitoring system (Holroyd et al., 2006; see Figure 5.1b).

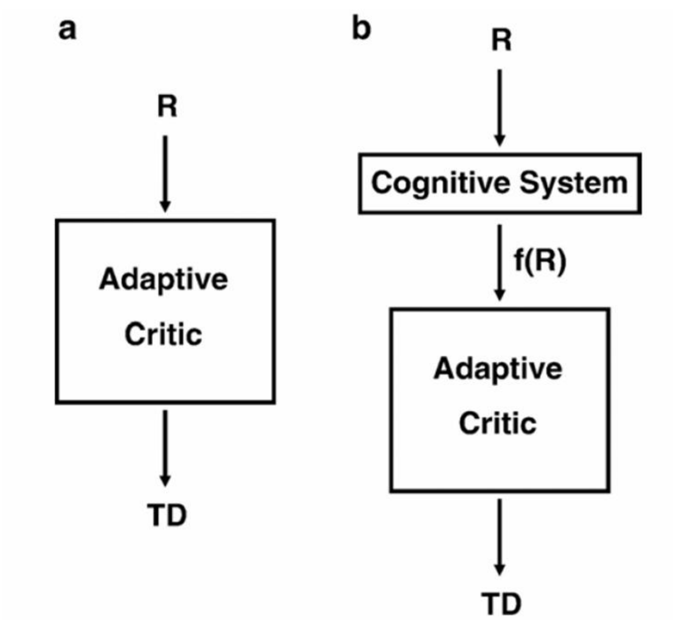


Figure 5.1 An illustration of the standard (left) and modified (right) adaptive critic in the monitoring system proposed by the RL-ERN theory. From Holroyd et al. (2006).

The cognitive system produces some function indicating whether or not the goal has been satisfied, and this information is further conveyed to the monitoring system, which computes the temporal difference in a binary manner. However the revised model did not define what criteria the cognitive system uses to judge whether the goal has not been satisfied or not. A perceptual mismatch hypothesis could provide the criteria for the cognitive system to produce the appropriate signal to the monitoring system. The schematic graph about the perceptual mismatch hypothesis is plotted in Figure 5.2.

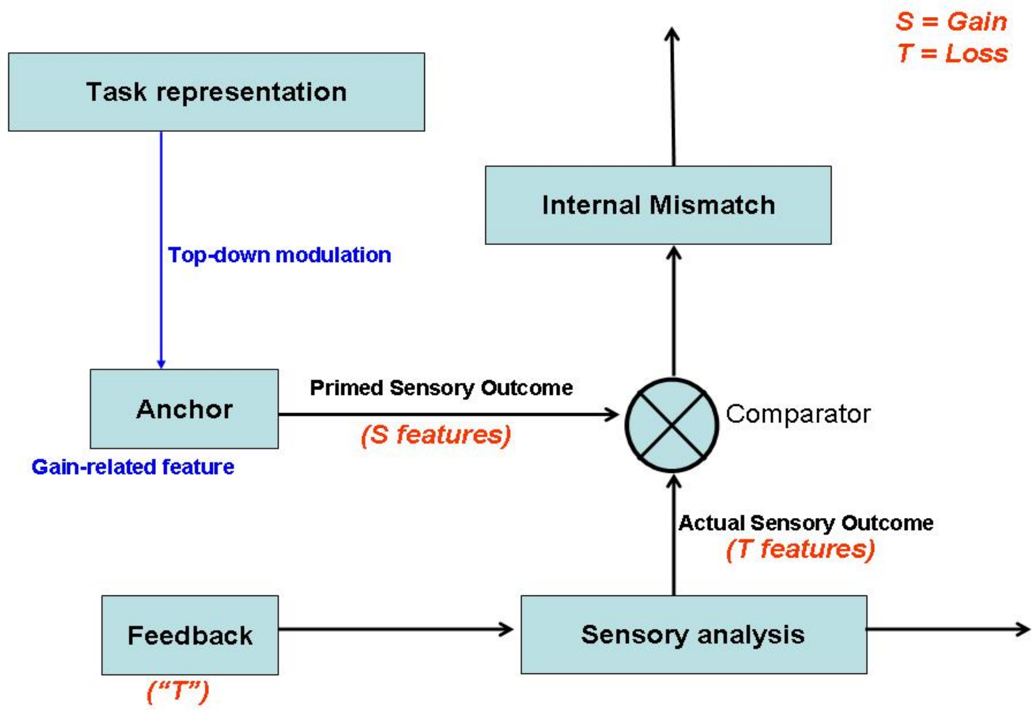


Figure 5.2. An illustration of the perceptual mismatch hypothesis in a gambling task. This model could be placed in the cognitive system in Figure 5.1 b.

For example, in a gambling task, participants are instructed to make a decision on which gamble to choose (e.g., two doors appearing on the screen) and then they receive letter feedback indicating whether they won or lost money during that trial (e.g., S indicates a gain and T indicates a loss). The feedback stimuli go through sensory analysis and the actual sensory outcome is compared to the primed sensory anchor outcome. It is hypothesized that in most cases task representation module directs gain-related perceptual features serve as the anchor since in the gambling task most participants hope to see the *gain* feedback rather than something else. A mismatch signal will be sent to the monitoring system upon the detection of the perceptual mismatch between the actual outcome and the gain perceptual tuning in the perceptual system. The monitoring system further interprets the mismatch as an error signal and communicates with the ACC to elicit the FRN. Thus this perceptual model could be placed in the cognitive system before the monitoring system in the RL-ERN theory (see Figure 5.1 b) to serve as a quick mechanism to produce the outcome function to the monitoring system. At the same time, it may exist independently of RL-ERN theory, and be used by other models in which the detection of the mismatch signal is necessary.

In addition to the mismatch produced by the comparator in which the actual sensory outcome and primed sensory outcome are compared, there is another mismatch detection embedded in the model. As Figure 5.3 shows, when the feedback stimuli comprises incongruent letters, an external mismatch signal will be produced through a second comparator, which could be further conveyed to the monitoring system like the internal mismatch and lead to the elicitation of the FRN in the ACC.

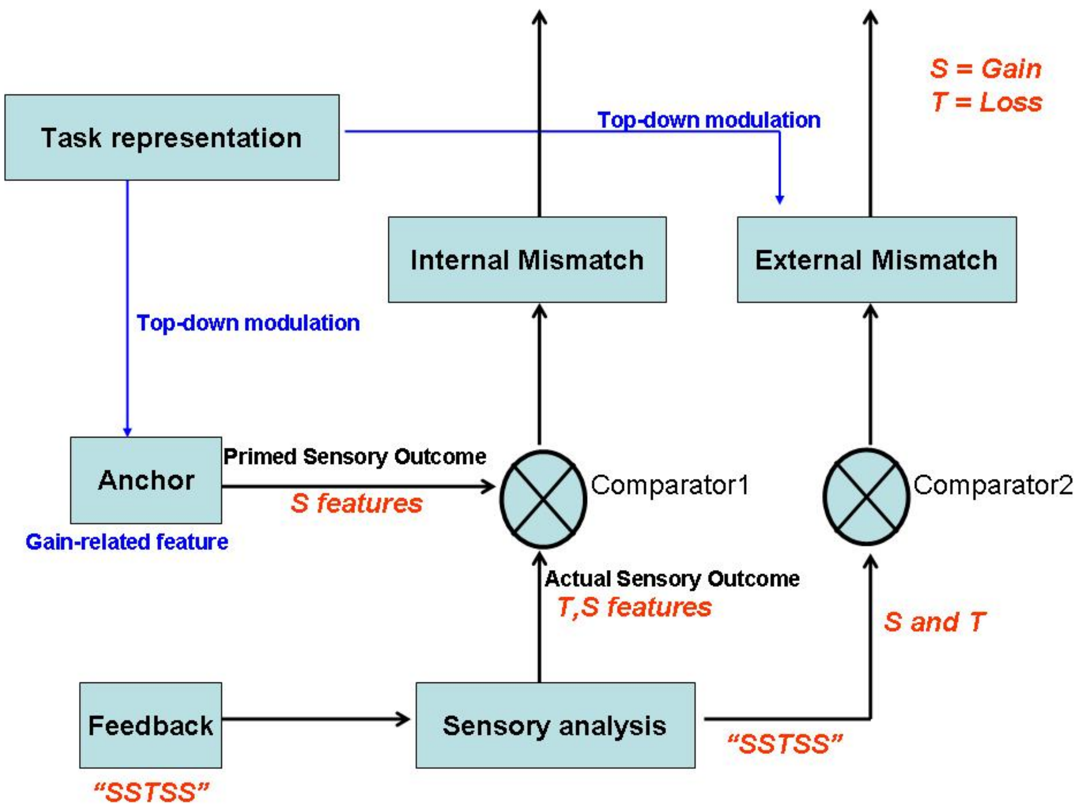


Figure 5.3 An illustration of the perceptual mismatch hypothesis in a gambling task including both the internal and external mismatch.

Experiment 7 further showed that the external mismatch that enhanced the FRN has to be produced by two reward representations. The task representation module stores the relevant reward information and imposes the top-down modulation on the external mismatch. When target and flanker letters connect to certain reward representations, the external mismatch will lead to the enhancement of the FRN. In contrast, when target and flanker letters have no certain reward representations as in unknown condition in Experiment 7, the external mismatch will not contribute to the FRN effect.

Interpretation of the empirical FRN results

This model could easily interpret the findings from numerous studies that both the *neutral* and *loss* feedback elicit a larger FRN than *gain* feedback but there is no FRN difference between *neutral* and *loss* feedback (Holroyd et al., 2004, 2006; Hajcak et al., 2006). According to the perceptual mismatch model, both the *neutral* and *loss* feedback include non-gain-related features, and the perceptual mismatch between the actual neutral/loss feedback and gain-related features in the anchor leads to the elicitation of the FRN. The model can also accommodate the result that the FRN amplitude is determined by the outcome value relative to the range of possible outcomes rather than the absolute value of the outcomes (Holroyd et al., 2004). It could be assumed that participants would hope to get the best available outcome and under the perceptual mismatch hypothesis, the perceptual attributes related to the best available outcome serve as the anchor for comparison, and any other available outcomes elicit larger FRNs when the perceptual mismatch from the primed features in the anchor is detected, as demonstrated by the experimental findings of Holroyd et al.

Moreover, the model can explain the results that FRN amplitude is not sensitive to reward magnitude, which has been demonstrated by two independent studies so far. As mentioned above, for example, in Hajcak et al.'s (2006) paper, "++", "+", "-", and "--" were used to indicate large gain (gain 25 cents), small gain (gain 5 cents), small loss (lose 5 cents) and larger loss (lose 25 cents) feedback respectively. It is possible that in the experiment, the "+" features serve as the anchor for comparison, so that *loss* feedback elicited a larger FRN due to the perceptual mismatch between "+" and "-" no matter what magnitude it is of. It may be argued that "--" had larger perceptual mismatch from "+" than "-" did; however this difference between the degree of the perceptual mismatch may not be strong enough to cause a difference in the FRN amplitude. Future experiments could use “++”, “-”, “+”, and “--” to map large gain (gain 25 cents), small gain (gain 5 cents), small loss (lose 5 cents) and larger loss (lose 25 cents) feedback respectively to test how the FRN amplitude may be modulated by the reward magnitude, reward valence and the perceptual attributes of the feedback information.

In Yeung and Safney’s (2004) experiment, participants knew whether they were gambling on a big magnitude or small magnitude before they made a choice, and then they received *gain* feedback which was indicated by a “+” and a particular number (e.g., “+7”) or *loss* feedback which was indicated by a “-” and a particular number (e.g., “-36”). They found that the FRN was not sensitive to the reward magnitude. According to the perceptual mismatch hypothesis, “+” may be used to serve as an anchor and any mismatch from the “+” leads to the enhancement of the FRN regardless of the reward amplitude the number on the right denotes. In some sense, the feedback stimulus used in Yeung and Safney (2004), comprising a “+” (or “-”) and a number, is similar to the feedback used in Nieuwenhuis et al. (2004b) and in Gehring & Willoughby’s (2002) study, in which the feedback denoted the information from two dimensions—correct-error dimension and gain-loss dimension. As Nieuwenhuis et al.’s (2004) experiments demonstrated, only the dimension indicated by the salient color information was evaluated. Under the perceptual mismatch hypothesis, the anchor was the salient color which indicated the positive information (e.g., gain); any mismatch from this color would elicit a larger FRN whether it included positive information (e.g., correct choice) in another dimension or not. According to the same logic, in Yeung and Safney’s experiment, the “+/-” appears to be more salient than miscellaneous numbers (6 to 11, 32 to 40). So it is not surprising that “+” serves as the anchor and the FRN amplitude was only sensitive to the reward valence information the salient information denoted. Future studies could manipulate the salience of the reward magnitude relative to the reward valence, and examine whether the FRN may be enhanced by the reward magnitude in some experimental conditions.

According to the RL-ERN theory, the FRN represents the detection of unexpected and unfavorable outcomes (Holroyd and Coles, 2002), so one fundamental prediction of the theory is that larger FRNs are elicited by unexpected unfavorable outcomes than by expected unfavorable outcomes. This prediction has been confirmed by Holroyd et al.'s (2003) findings that infrequent negative outcomes had a larger FRN reward effect than frequent negative outcomes. It is not easy for the perceptual mismatch hypothesis to explain this result because in its model the gain-related perceptual attributes are hypothesized to serve as the anchor since participants hope to receive *gain* rather than *loss* feedback even in the condition where the *loss* is frequent. The probability information may not induce the change of the perceptual tuning in the anchor as it may participants' expectancy (or prediction). Backing up this idea, Hajcak et al. (2005a) failed to observe the effect of probability manipulation on the FRN in their experiments. As reviewed in the Introduction chapter, in subsequent research, Hajcak et al. (2007) observed the FRN expectancy effect only when participants' prediction was explicitly reported right before the presence of the feedback. Self-report of subjective prediction was a confounding factor in the experiment. When participants explicitly reported that they predicted a loss, the perceptual tuning in the anchor could be temporarily changed to the loss-related perceptual attributes because apparently the loss-related perceptual attributes become the center of the attention at that moment. When the self-report happened a little earlier, for example, before participants made a choice, no FRN expectancy effect was observed (Hajcak et al., 2007 Experiment 1). To summarize, the above FRN expectancy studies showed that the probability manipulation may affect the subjective prediction/expectancy about the reward information; the change of the prediction/ expectancy, however, does not necessarily affect the elicitation of the FRN, consistent with the perceptual mismatch hypothesis.

The P300 and the motivational significance theory

One consistent finding about P300 amplitude through all the seven experiments is that *gain* feedback elicited a larger P300 than *loss* feedback, consistent with the observations in experiments conducted by Hajcak and his colleagues (2005a, 2007). A similar result was also evident in the study by Holroyd et al. (2004), although they did not explicitly discuss it. However, contradicting this result, Ito et al. (1998a) reported that a larger P300 was observed in response to affectively negative images than in response to positive images that were matched according to subjective rating of arousal, suggesting that the P300 was sensitive to the negative valence of stimuli. Moreover, Hajcak et al. (2005a Experiment 2) and Yeung et al. (2005) did not observe the effect of valence on the P300 amplitude. Instead several studies (Yeung et al., 2004; Sato et al., 2005) showed that P300 increased in amplitude with reward magnitude (larger vs. small amount of gain/loss), irrespective of the reward valence. Taken together, there was no consistent evidence in previous studies as to (1) whether the P300 is sensitive to feedback valence or not, or (2) whether the P300 amplitude is larger for positive or negative outcomes.

Yeung et al. (2004) proposed that P300 amplitude may reflect an objective coding of reward magnitude. It is possible that the P300 is sensitive to reward magnitude, however it is hard to justify this through the above seven experiments since no manipulation was performed on reward magnitude. However it is hard to explain the effect of valence on P300 amplitude with this proposal. Yeung et al. (2004) provided another proposal that the larger P300 amplitude with larger reward amplitude may reflect increased motivational or affective significance of greater rewards and penalties. If this were the case, one may hypothesize that positive feedback is related to increased motivation and thus attracts more attention, and the enhanced P300 reflects the activation of the positive motivation system. This hypothesis initially seems at odds with the findings that increased P300 was observed when pictures with negative valence were shown. However, the task difference between their study and the current study may explain the differing results. In Ito et al.'s (1998a) study, they asked participants to observe and evaluate affectively neutral, positive or negative pictures and greater P300 was found for negative than for positive stimuli. They argued that it may be related to the negative bias existing in human's evaluative space (Cacioppo & Berntson, 1994; Cacioppo et al., 1997), that is, the negative motivational system tends to respond more intensely than the positive motivational system to comparable amounts of activation. The negative bias may be related to the evolutionarily adaptive fight-or-flight response to threatening stimuli (Cannon, 1929). In another paper, Ito et al. (1998b) proposed that when the level of motivational activation is low, the motivation to approach exceeds the motivation to withdraw. This tendency that the output from the positive motivational system is greater than negative motivational system is called the positivity offset. The gambling task used in this dissertation study may be categorized as a low motivational task compared to the significant meaning of the threatening stimuli in Ito et al's (1998a) picture-viewing task. Thus the larger P300 on positive valence may be attributed to the higher activation of the positive motivational system.

According to the motivational significance theory, both the negative bias and the positive offset exist in our evaluation space. When the motivational activation is high, e.g., seeing threatening stimuli, the negative bias is more dominant and the P300 is enhanced by stimuli of negative valence; when the motivational activation is low, e.g, receiving positive feedback in our gambling task, positive offset is more dominant and P300 is enhanced to stimuli of positive valence. The reason that the effect of valence on the P300 is not always observed may be that the motivation activation is in a level where the effects of negative bias and positive offset cancel out.

In addition, Hajcak et al. (2005a) suggested that the inconsistent experimental results on the P300 in their two experiments may have to do with subjective expectations regarding the frequency of positive and negative feedback. For instance, in their first experiment where they did not observe larger P300 on the positive versus negative feedback, subjects may have believed that positive feedback was more likely overall than negative feedback. Negative feedback was received as infrequent trials so that enhanced P300 amplitude to the positive feedback was obscured by the effects of expectation on the P300 amplitude to the subjective infrequency of the negative feedback.

As for the congruency P300 results, it is hard to incorporate into the motivational view. The relevant discussion was presented in Chapter IV discussion. It appears that multiple evaluative processes including reward valence, reward magnitude, stimuli frequency and congruency may contribute to the elicitation of the P300. Future research will be needed to tease apart these processes and to distinguish the neural mechanisms underlying them.

Evaluation

Seven experiments have been conducted to investigate perceptual tuning and feedback-related brain activity in gambling tasks. In some experiments, behavioral data analyses were conducted, and in all the experiments P300 results were reported. However, the focus of this study is on the feedback-related negativity. In other words, this study could better be categorized as ERPology of the FRN than anything else (Luck, 2006). There may be many psychological factors contributing to the elicitation of the FRN, and the special interest in this study is the perceptual properties of the feedback stimuli. This factor has been ignored by the dominant RL-ERN theory and has been assumed unimportant in many FRN experiments (Hajcak et al., 2006; Holoyd et al., 2003; Miltner et al., 1997; Holroyd et al., 2002) in which various perceptual properties were used to indicate the reward information in gambling or guessing tasks.

Through the seven experiments manipulating the perceptual properties of the feedback, converging evidence has been accumulated that the FRN is affected by the perceptual salience of the feedback stimuli, the perceptual similarity among the feedback stimuli and the perceptual interference existing in the feedback stimuli. A perceptual mismatch hypothesis was proposed to explain the role of perceptual properties of the feedback stimuli in elicitation of the FRN. This perceptual mismatch model could be placed in the cognitive system which communicates with the adaptive critic in the monitoring system in the RL-ERN theoretical framework. In this way other parts of the RL-ERN theory do not need to be changed in order to accommodate current experimental findings. Attempt has been made at interpreting the empirical findings of the FRN within the perceptual mismatch hypothesis.

However there were some conflicting FRN results across the seven experiments. For example, while incongruent gain consistently elicited a larger FRN than congruent gain feedback across the seven experiments, the congruency effect in the loss feedback was shown in some experiments but not other. It was proposed that the inconsistent congruency effect in loss feedback may have something to do with the net effect of (1) the external mismatch existing in the feedback stimuli, (2) the internal mismatch between the target loss in the actual outcome and the gain perceptual tuning in the perceptual system, and (3) the modulation effect of the presence of the gain-related flanker features in the incongruent loss feedback. The net effect in different experiments may be different due to different task representations; thus the inconsistent results may be interpretable but not predictable since it is hard to figure out all the details to actually compute a value for the net effect. As stated in Chapter IV discussion, there were also conflicting results regarding the P300 congruency effect. These issues are further complicated by the problems of component overlap between the FRN and the P300. Answers await future related ERP research.

One thing worth mentioning is that the FRN used in this dissertation study is a general term for the negative voltage deflection peaked around 200-400 ms following the onset of the feedback. It may comprise two components—the loss-related negativity and the interference-related negativity, corresponding to the internal mismatch and the external mismatch respectively produced by the two comparators in the perceptual mismatch model (see Figure 5.3). As shown in above experiments, these two components have similar latency window and scalp distribution, and both are sensitive to similar manipulations of perceptual properties and could be explained by the perceptual mismatch hypothesis. Thus in this study FRN is the unified name for them.

Conclusion

In this dissertation study, the role of perceptual properties of the feedback stimuli was evaluated in the elicitation of the FRN. Future studies using the FRN as the dependent variable have to consider the influence of the perceptual properties of the feedback stimuli. The FRN research is still in its infant stage considering its short history from Miltner et al's (1997) paper. More ERPological research of the FRN is needed to systematically examine various potential variables that may affect the elicitation of the FRN.

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