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UNIVERSITY OF CALIFORNIA

Los Angeles

The Neuropsychology of Executive Function: Hemispheric Contributions to Error Monitoring and Feedback Processing

A dissertation submitted in partial satisfaction of
the requirements for the degree Doctor of Philosophy
in Psychology

by

Jonas Todd Kaplan

2002

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Ann Arbor, MI 48106-1346

The dissertation of Jonas Todd Kaplan is approved.

Marco Iacoboni

Barbara Knowlton

Thomas Wickens

Eran Zaidel

Eran Zaidel, Committee Chair

University of California, Los Angeles

2002

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VITA

Dec 3, 1974	Born
1996	B.S. in Psychology University of Michigan, Ann Arbor
1996	UCLA University Fellowship
1997	M.A. in Psychology University of California, Los Angeles
1999	Shepard Ivory Franz Distinguished Teaching Assistant Award
2000	UCLA Collegium of University Teaching Fellows
2000	UCLA Campuswide Teaching Assistant Coordinator
2001	National Research Service Award (NRSA) Institutional Behavioral Neuroscience Training Grant

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ABSTRACT OF THE DISSERTATION

The Neuropsychology of Executive Function: Hemispheric Contributions to Error Monitoring and Feedback Processing

by

Jonas Todd Kaplan
Doctor of Philosophy in Psychology
University of California, Los Angeles, 2002
Professor Eran Zaidel, Chair

This dissertation investigates self-monitoring processes in the two cerebral hemispheres. A series of experiments in which performance feedback is presented to the left and right hemispheres during lateralized tasks examines the lateralization of metacognitive function. Several manipulations involving the type of cognitive task being monitored, the visual field of presentation, and the type of feedback stimulus presented show that the two hemispheres differ in their ability to process performance feedback. Results from lexical decision support a right hemisphere monitoring advantage in that task which depends on the type of feedback stimulus. In an object decision task, however, there is a different reaction to lateralized feedback, with performance affected most strongly when feedback is presented to the left hemisphere. Behavioral data are combined with functional magnetic resonance imaging and testing of split-brain patients to further elucidate the neural mechanisms of hemispheric monitoring. Split-brain patients were unable to correct their errors with either hemisphere, suggesting that interhemispheric communication may be necessary for error correction. Neuroimaging data indicate that feedback processing recruits neural networks for sensorimotor integration. Taken together, these results show that self-monitoring in the hemispheres is a complex, multi-faceted phenomenon that involves both interhemispheric independence and cooperation.

The Neuropsychology of Executive Function: Hemispheric Contributions to Error Monitoring and Feedback Processing

The central goal of this research is to elucidate the mechanisms by which each hemisphere of the human brain monitors its own behavior and cognition. Since the left and right hemispheres often function independently, they can be expected to have their own executive control systems. The two hemispheres have different ways of handling information, and we may expect that the disparity in cognitive style between them should extend to their monitoring and control processes. More specifically, this research investigates how each hemisphere monitors for errors, and how feedback information about errors is used to modify behavior.

GENERAL BACKGROUND

EXECUTIVE FUNCTION

Making mistakes is part of life. On a daily basis we experience all kinds of small and large failures. We watch as our fingers hit the wrong letters on the keyboard, we hear the grinding metal as we push the gearshaft into the wrong gear, and we listen as the words coming out of our mouths fail to convey what we intended. Our behavior is so complex and unreliable that we must be able to monitor our actions to see if they accord with our intended goals. We must also be able to alter our behavior based on what we observe, to adjust our actions based on continually changing feedback. According to Arbib (2002), the term “action” refers to a movement that is associated with a goal or expectation. In this sense, the outcome of every action that is executed can be checked against its intended goals to determine its success or failure.

In cognitive science, the processes of monitoring and responding to errors are often called *executive* functions. The "executive" label connotes an analogy to the executive of a company or of a government, who oversees the operations of the organization, making sure that everything runs smoothly. The executive not only keeps track of what is going on in the various departments and sub-units of the organization, but makes important decisions and allocations that determine its policies and ultimately its success. In the brain, the executive would be able to assign priority to tasks and goals, distribute resources (i.e. attention) and monitor the progress of behavior. A further elaboration of the executive processes comes from Kluwe (1982), who made a distinction between executive monitoring and executive regulation (See Table 1). According to Kluwe, executive monitoring includes identification of the present task, checking progress as it goes, evaluating alternatives, and predicting results. Executive regulation involves allocating resources, deciding what to do, and regulating the amount, intensity, and speed of processing.

It is important not to take this analogy too literally. The brain may have no one president, no single CEO. Nevertheless, it does end up accomplishing the tasks that such a figure would be responsible for. Understanding how it does so is the central goal of this dissertation. In a corporation, each department has its own monitoring system in addition to the central monitoring undertaken by the executive staff. The financial people check their numbers for errors several times before sending them up the line. Do subsystems in the brain have their own monitors too? This is an important theoretical question for cognitive neuroscience. Is there a "central" monitoring system *and* localized specialty monitors? If so, how are they integrated? A paradigm case for examining these issues involves the most salient subdivision in the human brain, the left and right cerebral hemispheres. The two hemispheres often function as fully independent cognitive systems, each with its own perceptual machinery, memories, language system, and motor control (Zaidel, Clarke, & Suyenobu, 1990). It follows that each hemisphere may have its own executive control as well. My research focuses on error monitoring and feedback processing as examples of executive functions in the hemispheres.

Table 1: Kluwe's (1982) taxonomy of executive function

EXECUTIVE MONITORING	EXECUTIVE REGULATION
1. Identification (What am I doing?)	1. Regulation of resources (Allocation of resources)
2. Checking (Did I succeed? Do I make progress?)	2. Regulation of the subject (What should I work on?)
3. Evaluation (Are there better alternatives? Is my plan good?)	3. Regulation of the intensity (Amount of information that is processed; duration and persistence of processing)
4. Prediction (What could I do? What will result?)	4. Regulation of the speed of information processing (Skip or add steps in the problem solving;

BEHAVIORAL EVIDENCE FOR ERROR MONITORING

Several lines of evidence suggest that there are a specific set of processes in the brain concerned with the detection and correction of errors. In the 1960's and 1970's Patrick Rabbitt conducted a series of behavioral experiments using the choice reaction time paradigm (Rabbitt, 1966a, 1966b; Rabbitt & Phillips, 1967; Rabbitt & Rodgers, 1977; Rabbitt & Vyas, 1970). Choice reaction time is relatively simple: the participant must distinguish among the stimuli by responding with an appropriate choice as quickly and as accurately as possible. For example, in one experiment the numbers '4' and '5' appeared one at a time on a computer screen, and the participant pressed one key if they saw a '4' and another key if they saw a '5'. Rabbitt found that when participants made errors, they tended to slow down on the following trial. Participants were not given any feedback, so the post-error slowdown is interpreted as spontaneous self-monitoring in this task (Rabbitt & Vyas, 1970). Since the participant has reacted to the error by slowing down, we can say he or she has at least implicit knowledge of the error.

It is not clear from these experiments why participants slow down after making errors, but it is generally interpreted as resulting from some ongoing monitoring or compensation for the error (Gehring, Coles, Meyer, & Donchin, 1994). Other experiments with choice reaction time tasks have shown that participants do often have explicit awareness of their errors. For example, Kopp & Rist (1999) told participants to correct their errors in a choice reaction time task by pressing the correct button after a mistake. Corrected errors accounted for about 14% of the trials, while uncorrected errors were very rare, occurring only on about 1% of trials. However, awareness of errors may depend on the type of error being made. Scheffers & Coles (2000) argue that errors in speeded reaction time tasks are often a result of premature responding; the participant guesses too quickly and makes an error. These types of errors should be more correctable than errors that are due to perceptual or cognitive processing limitations. According to Scheffers & Coles, if an error is a result of a response made before all the appropriate information is processed, a monitoring system should be able identify the error once all the information has been completely processed. A comparison can then be made between the executed response and the current, completely up-to-date information. The details of this type of model of error detection will be discussed in detail below. However, if an error is due to poor processing of the stimulus, how can the monitor ever know what the appropriate response should have been?

One possibility is suggested by Zaidel (1987). Error monitoring could take place if two modules are simultaneously engaged in the same computation. A comparison between the results of the two parallel computations gives a measure of confidence in the result. Corresponding functional modules in the two hemispheres would be well suited for this type of monitoring since they may both be capable of the same type of processing, though perhaps using different strategies.

Despite our limited understanding how error monitoring is managed, it is behaviorally evident that there is some type of error monitoring going on. Participants can detect and correct their errors in a choice reaction time task, and even when they are not asked to do so their behavior shows evidence of monitoring. This is in accord with anecdotal evidence; when participants are run in our laboratory experiments, they often react to their mistakes by swearing, apologizing, or giggling even in the absence of feedback. Only recently have we begun to understand the neural networks that accomplish error monitoring. I will review the current literature on the neural mechanisms of error monitoring before discussing the possible hemispheric differences in contributions to these functions.

ERROR MONITORING AND THE MEDIAL PREFRONTAL CORTEX

Early evidence of a neural system for detecting and responding to errors came from event-related potential (ERP) work in the early 1990's. It was noticed that if event-related analyses were locked to the response rather than to the stimulus onset, a clear difference in the electrical signal between correct and incorrect trials emerged (Falkenstein, Hohnsbein, & Hoorman, 1995; Falkenstein, Hohnsbein, Hoorman, & Blanke, 1991; Gehring et al., 1994; Gehring, Goss, Coles, Meyer, & Donchin, 1993). Most often these experiments used a specific type of choice reaction time task known as the Eriksen flankers task, after Eriksen and Eriksen (1974). This task presents a string of letters as the stimulus, and the participant must identify the central letter. The surrounding letters are known as the flankers, and they can be either the same as the target, or different. For example, the participant may see "HHSHH" or "SSSSS", and would respond in both cases by pressing the key corresponding to the letter 'S', the central letter. Responses are faster when the flankers are compatible with the target, and the incompatible condition tends to produce a good amount of errors when participants are under instructions to respond quickly. This task and its variations have become standard in error processing research because they are simple, yet they produce response conflict, which leads participants to make mistakes.

The difference between the ERP on correct responses as compared to incorrect responses is shown in Figure 1. There is a negative peak in the waveform for error trials that begins at the response and peaks about 100 - 150 ms later which has been called the Error-Related Negativity (ERN) by Gehring et al. (1994) and the Ne by Falkenstein et al. (1995). For clarity I will refer to the component as the ERN, but this is the same component that is also called Ne in the literature. The ERN is largest at electrodes

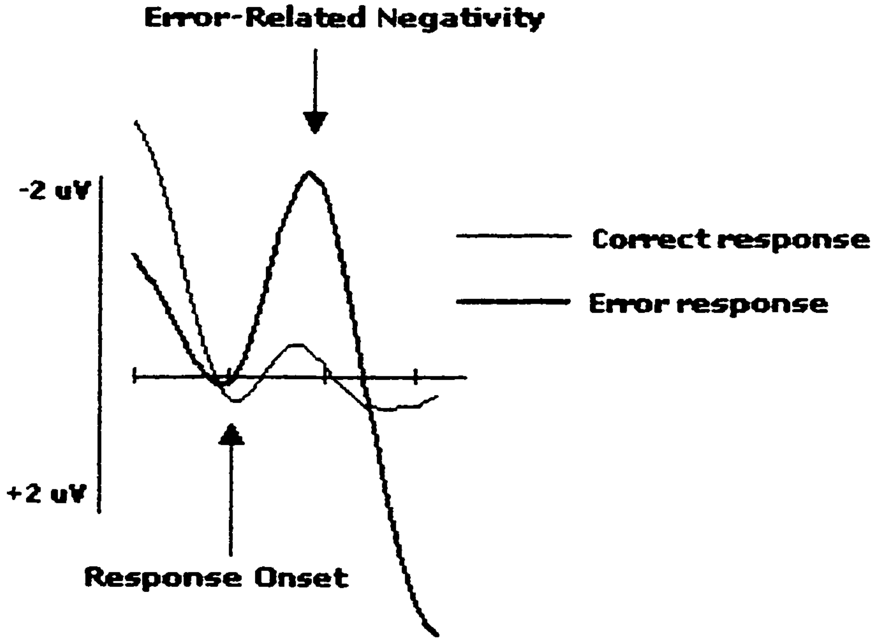


Figure 1: The Error-Related Negativity (ERN)
A negative peak is seen in the waveform for error trials.

towards the front and center of the scalp. This component was originally interpreted by Gehring et al. as the manifestation of a central error-monitoring mechanism in the brain, but as will be discussed below the current interpretation of the ERN is growing more complex.

While ERP methods do not provide the best means of localizing the source of brain activity, there is mounting evidence that the ERN originates from a region of the medial prefrontal cortex known as the anterior cingulate cortex (ACC). Using source dipole localization techniques, Dehaene, Posner, and Tucker (1994) concluded that the pattern of scalp activity generated by the ERN is consistent with an anterior cingulate source. This is corroborated by data from single-cell recordings in monkeys showing error-related activity in the ACC (Paus, 2001). Recently, several neuroimaging studies using event-related designs have confirmed that there is ACC activity in the human brain related to the commission of errors (Kiehl, Liddle, & Hopfinger, 2000; Menon, Adleman, White, Glover, & Reiss, 2001).

Gehring et al. (1994) argued that the ERN was an indication of error processing based on evidence from several experimental manipulations and analyses. First, they manipulated how important accuracy was to the participants by means of a financial reward system. In some blocks, participants were encouraged to respond quickly and recklessly as they were rewarded for fast responses and not heavily penalized for errors. In other bocks, accuracy was emphasized, since there was little reward for fast responses, and a large penalty for errors. Results showed that the amplitude of the ERN was greater in the condition where accuracy was important to the participants. That is, in the condition where participants need to pay more attention to the correctness of their responses, the ERN was larger.

Responses in these experiments were recorded with a device that measured the force of the response; participants would squeeze the recording device and the experimenters could analyze the amount of squeeze as it related to the ERP data. The data showed that larger ERNs were associated with weaker error responses. This suggested that the ERN is involved in interrupting or changing the erroneous response. Furthermore, large ERNs were also associated with an increased probability of error correction. This evidence seems to suggest that the ERN is related to the detection and correction of errors.

However, a study of the ERN on a go/no-go task casts doubt on the component's relationship to error correction (Scheffers, Coles, Bernstein, Gehring, & Donchin, 1996). In this experiment, there are two types of error possible. A participant can fail to respond to a "go" stimulus, or he or she can erroneously respond to a "no-go" stimulus. A response to a "no-go" stimulus is not a correctable error: you cannot undo your action. Still, the ERN was present with both types of errors and did not differ in amplitude. The authors conclude that the ERN is more likely related to the *detection* than the *correction* of errors, since it is present even in the case where an error cannot be corrected.

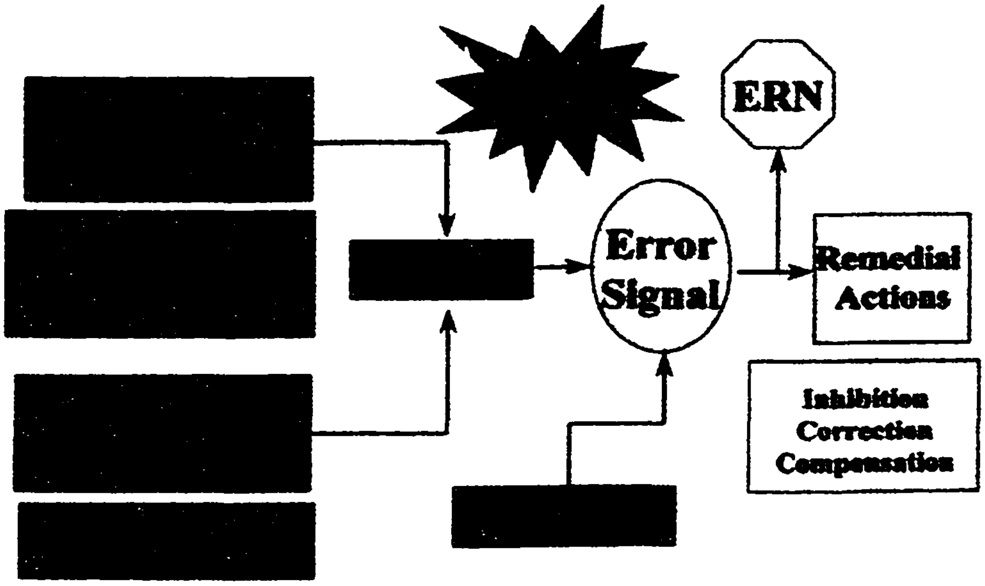


Figure 2: A model of error monitoring modified from Coles, Scheffers, & Holroyd (2001)

The green areas represent operations concerned with IMPLICIT monitoring. Blue areas represent EXPLICIT monitoring. Yellow indicates operations common to both kinds of monitoring.

To further understand the functional significance of the ERN it will be useful to develop further a model of how error detection and correction take place. Figure 2 presents a model of error monitoring adapted from Coles, Sheffers, & Holroyd (2001). Theoretically there two ways that monitoring systems can obtain information that an error has occurred. First, explicit error feedback can be provided to sensory systems. I refer to this as *explicit monitoring*, since information about errors is provided and the brain does not need to determine on its own that an error has taken place (Kaplan & Zaidel, 2001). This is indicated in blue in Figure 2. Imagine a piano teacher watching over her student and pointing out exactly when a wrong note is played. In this case, the student does not need to monitor for errors, but only to react to the signal that one has occurred.

Secondly, internal monitoring may take place in the absence of explicit feedback. I will call this *implicit monitoring.* In most of the experimental choice reaction-time tasks feedback is not provided, but subjects show behavioral slowing and a negative electrical potential on error trials.

One way that implicit monitoring can be accomplished is through a comparison between the executed response and some representation of what the response should have been. The question here is: was the action I just executed the right one? A monitoring system should have access to motor "efferent copies" of the motor commands sent out to the spinal cord for comparison with the newly updated results of cognitive computations (Coles, Scheffers, & Holroyd, 2001; Heilman, 1991; Scheffers & Coles, 2000). The idea of an internal copy of motor commands was originally described by Sperry (1950), who called it "corollary discharge". A representation of the correct response may come from redoing a computation and comparing the result (Measso & Zaidel, 1990), computation by a parallel module (Zaidel, 1987), or if an error is made due to premature responding, completion of processing. This latter type of monitoring is likely to take place in speeded choice reaction time tasks where many errors are a result of quick responses, like the ones used in the electrophysiological experiments.

In this model, the ERN represents a signal that an error has occurred — regardless of how this was determined. Milnter, Braun, & Coles (1997) have shown that the ERN occurs in response to negative feedback signals, indicating that it is involved in explicit monitoring as well as implicit monitoring. The ERN seems to reflect a central monitoring process that is generic across cognitive domains: in addition to showing up in the flankers task, the ERN has been found for errors in the Stroop task (Gehring & Fencsik, 2001), a memory task (Gehring et al., 1994), a categorization task (Scheffers et al., 1996), for vocalization errors (Masaki, Tanaka, Takasawa, & Yamazaki, 2001), and for foot as well as hand responses (Holroyd, Dien, & Coles, 1998).

CONFLICT MONITORING VS. ERROR MONITORING

It is possible, however, that the ERN does not reflect error processing per se, but instead some other process that tends to lead to more errors. The conflict monitoring theory claims that the anterior cingulate monitors the conflict generated by competing motor responses in order to signal the need for top-down control (Carter, Braver, Barch, Botvinick, & Cohen, 1998; Cohen, Botvinick, & Carter, 2000). Situations in which there is greater response conflict would tend to lead to more errors, hence the "error-related" negativity.

There is considerable support for this view. Carter et al (1998) found increased ACC activity in a task designed to generate response conflict. This activity was found on correct as well as incorrect trials as long as there were two competing responses elicited by the stimulus. Gehring and Fencsik (2001) pitted the error detection and response competition theories against each other by manipulating the degree of similarity between motor responses required by the task. They used a Stroop task in which subjects could respond with their right or left hand or foot. According to the error detection theory, the ERN reflects the degree to which the executed response deviates from the correct response, so the ERN should be larger when the error response is considerably different from the correct response (for example when the correct response is the right hand and an error is made with the left foot). On the other hand, the response conflict theory predicts that responses which are more similar should produce more conflict and hence a larger ERN. Gehring and Fenscik found larger ERNs when the error response was more similar to the correct response, supporting the response conflict theory.

Still, there are several findings that the response conflict account has difficulty explaining. First, the ERN is seen following explicit error feedback (Milnter et al., 1997), well after the response has been completed. Secondly, as described earlier, making accuracy important to subjects relative to speed increases the size of the ERN (Gehring et al., 1993). Falkenstein at al. (2000) have argued that the lateralized readiness potential (LRP) is an index of response conflict, and that the size of the ERN is independent of this measure. Furthermore, error-related activity is often found in go/no-go tasks, where only one response needs to be prepared (Kiehl et al., 2000; Scheffers et al., 1996). In this case, the conflict monitoring theorist would have to claim that the inhibition of a response conflicts with the execution of the same response. Similarly, ERNs are elicited when subjects make responses that are too slow, even though their response selection was correct (Luu, Flaisch, & Tucker, 2000).

At the very least this system seems to be involved in monitoring some aspect of motor function that is relevant to error monitoring. Yet to date a coherent account of the central functional role of the ACC activity has not emerged. The most recent evidence suggests that the ERN may be more related to affective processing than to conflict processing. An experiment by Gehring and Willoughby (2002) found ERNs when subjects lost money in a gambling task, even if the decision was not an "error". In this experiment subjects saw two numbers on a screen, each within a square. Each number could be either 5 or 25, and corresponded to the amount of money in cents the subject could win or lose by choosing that box. After making a choice, the squares turned green or red indicating that the subject had gained or lost money. Thus, in some circumstances, subjects lost money, but had actually made the best choice since they chose the lesser of the two numbers. The negative ERP potential was related to the notification of loss rather than to an incorrect choice. It has also been shown that negative mood can modulate the ERN (Luu, Collins, & Tucker, 2000). It may be that the ERN signal reflects that whatever has happened is not in accordance with current motivations and goals. The relation of self-monitoring to emotional processing is particularly relevant to questions of hemispheric specialization for executive functions, since there are clearly differences in emotional processing between the two hemispheres (Davidson, 1995).

The anatomy of the anterior cingulate cortex confirms that it is in a position to integrate cognitive, affective, and motor behavior (Bush, Luu, & Posner, 2000; Paus, 2001). The ACC has connections with the limbic system, the lateral prefrontal cortex, and several motor areas including the premotor and supplementary motor areas. However, no single brain region functions on its own without being integrated into a larger circuitry for behavior, so it is important to review the broader neural network with which the ACC must interact to accomplish self-monitoring.

BEYOND THE ACC: A NEURAL NETWORK FOR MONITORING AND CONTROL

Despite the considerable recent evidence pointing towards the anterior cingulate, neuropsychological theories have traditionally located executive functions in other frontal lobe regions including the lateral prefrontal cortex and the orbital prefrontal cortex (e.g. Luria, 1966; Norman & Shallice, 1986; Shallice, 1988; Stuss & Benson, 1987). The ACC has dense interconnections with the lateral prefrontal regions, and neuroimaging studies frequently find co-activation of the two regions (Koski & Paus, 2000; Paus, 2001). For example, dorsolateral prefrontal cortex and anterior cingulate cortex are both active when subjects are instructed to pay attention to their performance of an overlearned motor task (Jueptner et al., 1994). The lateral prefrontal areas are ideally situated to perform executive functions; they have widespread reciprocal connections with many other regions of the brain, including the thalamus, hypothalamus, amygdala, hippocampus, basal ganglia, and several distant cortical regions (A Damasio, 1985). The prefrontal cortex (PFC) is the only area connected to five sensory areas, which means it has access to the necessary sensory information for monitoring (Stuss & Benson, 1984). Various executive functions have been attributed to the prefrontal cortex, including planning, sequencing of actions, monitoring of behavior, inhibition of inappropriate or unwanted action, and personality (A. Damasio, 1985; Stuss & Benson, 1984). Patients with prefrontal damage are typically disorganized, impulsive, and unreliable. They often experience drastic personality changes, exhibit socially inappropriate behavior, and have difficulty making decisions that seem simple to others. Their social and professional lives, poorly managed after the brain injury, are often destroyed despite seemingly intact intelligence (A Damasio, 1985; Luria, 1966; Stuss & Benson, 1984, 1987). But while stories of the strange behavior of frontal lobe patients abound, it has been difficult to capture the heart of the deficit experimentally and to pin down the exact functions of the prefrontal cortex.

One of the first direct tests of error monitoring in a frontal patient was conducted by Konow & Pribram (1970). When asked to draw a square, their patient drew a circle instead. She immediately reported that she had not drawn a square, but continued to draw circles over and over, perseveratively. Another time, the patient drew the letter "A" and said at the same time "That's not a square—I guess I'll draw you an 'A'" (p. 490). Konow & Pribram draw the distinction between recognizing errors and utilizing error information. Clearly in this case the patient can recognize her errors, but cannot utilize the information to change her behavior. The suggestion is that the frontal lobes are involved in *compensating for errors* rather than *monitoring for errors*. Further evidence for this view comes from Jarvie (1954), who describes six frontal patients. These patients could describe the personality changes that accompanied their brain damage, but were unable to do anything about it. Under Kluwe's taxonomy of executive function, we would classify these as executive regulation processes as opposed to executive monitoring processes.

Luria's theory of frontal lobe function stresses the control and organization of action as the primary function of the frontal lobes (Luria, 1966; Luria & Homskaya, 1964). He claimed that while frontal patients have the ability to execute individual motor acts, they lack the ability to organize these individual acts appropriately. This was perhaps best demonstrated by Lhermitte, Derousne, & Signoret (1972, described in Stuss & Benson, 1984) who studied four frontal patients. The patients were asked to copy the Rey Figure, a complex figure used to test memory. They had great difficulty with the figure unless it was broken down into sections, so that they only had to complete one part of the figure at a time. Providing this sort of structure allowed the patients to complete the figure satisfactorily.

This type of planning and organization of behavior is precisely what is needed when an error occurs. When we make a mistake, we need to figure out what the appropriate remedy is and execute it. Luria believed that the frontal patients could not use their internal speech to guide their actions:

> They give rise to a severe disturbance of a different function of speech, namely its regulatory function; the patient can no longer direct and control his behavior with the aid of speech, either his own or that of another person. (Luria, 1973, p. 211, quoted in Stuss, 1990)

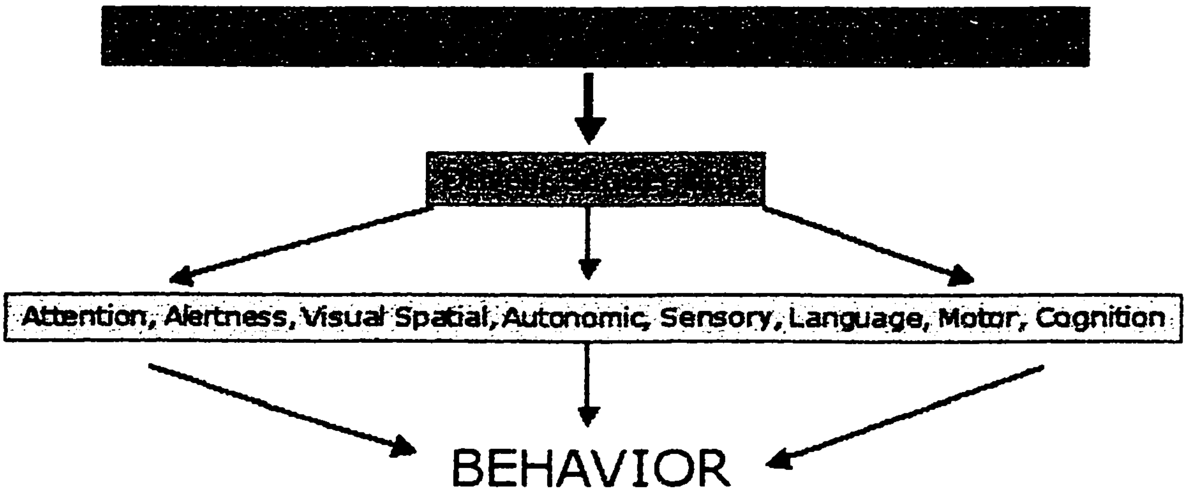
Milner (1963; Milner & Petrides, 1984) has argued that Luria's interpretation is too narrow, that the frontal deficit is really in using external cues, not just speech, to regulate behavior. Milner and Petrides (1984) describe a maze learning task in which participants must use trial and error to find the correct route. Feedback is given auditorily; a buzzer goes off when the participant makes a wrong turn. In this case the signal is non-verbal, yet frontal patients learn much more slowly than controls. Also along these lines, Milner (1963) describes the performance of frontal patients on the

Wisconsin Card Sorting Task, which has since become a standard test of frontal lobe function. In the task, participants must sort a series of cards with colored shapes on them. The cards may be sorted by number, color, or shape; it is the participant's task to determine, through trial and error, which is the correct category. The experimenter gives verbal feedback. Once the participant sorts ten cards in a row correctly, the criterion is suddenly changed. Now, to the participant's surprise, the cards must be sorted according to a different category. This procedure continues six times. Milner tested a large group of frontal patients, 94 in total, with lesions in different regions of the frontal lobes. Most of the patients were tested both before and after the surgery that caused the lesion. Milner found that the worst performance was in those patients with dorso-lateral lesions, and that the errors were mainly perseverative errors. That is, the patients continued to sort according to the old category despite the experimenter repeatedly saying "wrong". Milner also reports that many patients were able to say what their responses should be, but were still unable to make the correct response. The patients seem to know that they are making the wrong response, but they simply cannot change their behavior based on this information. Again we see in the frontal patient the dissociation between monitoring for errors and the ability to correct them. Milner's original results with the Wisconsin Card Sorting Test have been replicated many times (Faglioni, 1999). In fact, there have been many studies in which frontal patients are required to learn by trial and error, and in general they are impaired (Faglioni, 1999).

Several theorists have attempted to formalize the organizational/executive processes of the frontal lobe into explicit hierarchical theories. Stuss & Benson's model

(Stuss, 1991; Stuss & Benson, 1984, 1987, 1990) is one of the most popular. The model is depicted in Figure 3. At the highest level, executive function involves anticipation, goal selection, planning, and monitoring. These functions preside over the next level, drives and sequencing, which are in turn connected to particular behaviors.

Figure 3: Stuss & Benson's (1984) Hierarchical Model



At this time it will be useful to refer to the distinction made by Shiffrin & Schneider (1977) between automatic and controlled processes. Automatic processes are fast, overlearned routines that are easily triggered by stimuli. Controlled processes are slow, deliberate, conscious, and require attention. According to Stuss & Benson, automatic processes are served by posterior or basal brain regions, while controlled, conscious processes are handled by the frontal lobes. The highest level of function in their hierarchy, then, is the work of the frontal lobes. Notice that this model attributes monitoring functions as well as action-controlling functions to the frontal lobes. There is, however, little evidence to support direct participation by the frontal lobes in monitoring. This model is also abstract in that it does not specify the method by which the highest level functions are accomplished. It is therefore difficult to formulate specific testable predictions based upon the Stuss & Benson model.

A more useful model has been developed by Norman and Shallice (Norman & Shallice, 1986; Shallice, 1988; Shallice & Burgess, 1991). Like the Stuss & Benson model, this model also makes use of the distinction between automatic and controlled processes, as well as a supposing a hierarchy of function. However, the specifics of the control processes are laid out in detail. The main assumption of the model is that various schemata (fixed patterns of behavior) compete for access to effector systems. Two control mechanisms decide which action will be executed. The first is "contention scheduling", in which local competition between schemata determines a winner based on level of activation. Activation is usually stimulus-driven—for example a red light while driving activates a brake response. Contention scheduling is thus useful in routine situations, and is fast and automatic. The second system comes into play in non-routine situations when the "default" behavior is undesirable. This system is called the Supervisory Attentional System (SAS), and it can override contention scheduling.

It is the SAS that Shallice attributes to the frontal lobes. There are then some predictions about what would occur in the absence of the SAS. Behavior would be driven completely by contention scheduling, and would thus be participant to the properties of that system. Shallice argues that since contention scheduling only deals with routinized tasks, it is slow to change. That is, if an action is triggered by a stimulus, that same action is likely to be triggered again by the same stimulus, regardless of the consequences of the action. As Shallice puts it, "The system driven by contention scheduling alone should behave in rigid fashion." (1988, p. 339) This, of course, explains the perseverative errors of frontal patients on the Wisconsin Card Sort task and in other situations as well. In fact, frontal patients have often been described as "stuck-in-set" (Darling, Sala, Gray, & Trivelli, 1998).

Also, since contention scheduling is so stimulus-driven, behavior should be easily evoked by irrelevant stimuli. In addition to clinical reports of "distractibility" (Eslinger & Damasio, 1985) there exists a phenomenon known as "utilization behavior" in which frontal patients use an object simply because it is present, even if there is no reason to use it. For example, an empty glass put within reach of a frontal patient may be automatically grasped (Shallice, 1988). It is as if a schema is inappropriately executed due to the lack of an SAS.

The involvement of the frontal lobes in error correction is consistent with this model —compensation for errors may be considered one of the roles of the SAS. The SAS may override contention scheduling on the basis of information gained from an error monitoring process. The rigidity of the contention scheduling program implies insensitivity to feedback, while the SAS is capable of organizing and changing behavior on the fly.

The stimulus-driven aspect of the frontal lobe syndrome and insensitivity to feedback are corroborated by a study from Bechara, Damasio, Damasio, and Anderson

(1994). In this study patients with orbitofrontal frontal lesions participated in a card game in which they repeatedly selected cards from one of four decks. Each card provided a monetary reward or penalty, and the goal was to earn the most money. Two of the decks provided small but consistent rewards ($50) mixed with small penalties. The other two decks gave larger rewards ($100) but were not good bets in the long run because they contained large penalties as well. Control participants consistently learned to draw from the "good" decks, the ones that gave smaller rewards but yielded a greater profit in the end. Frontal patients drew more from the "bad" decks and ended up losing money overall. The patients were drawn to the immediate reward, but could not adjust their selection based on the consequences of their choices (i.e. the penalties). The authors describe the frontal patients as being "insensitive to future consequences". They argue that the patients have access to the information about the consequences of their behavior, *but fail to act upon it.* Evidence that these patients have knowledge of the consequences of their actions comes from an additional study by Bechara, Tranel, Damasio and Damasio (1996) in which skin conductance response (SCR) was measured during the same gambling task. Frontal patients showed a normal SCR response to the penalties. However, they did not show the same anticipatory SCR change when reaching for the dangerous deck that normal participants showed.

How the PFC interacts with the ACC in monitoring and control is not well understood. It is tempting to draw the conclusion that the ACC is involved in detecting errors, while the PFC initiates behavioral and cognitive responses to error information. However, there is data suggesting a more complex interaction between the two regions.

Gehring and Knight (2000) recorded the error-related negativity (ERN) from patients with lateral PFC damage and found that there was ERN activity on correct trials as well as on error trials. There is, then, an interaction between these two areas that is necessary for error monitoring. It may be that the error signal is indiscriminant in frontal patients because of a failure to represent current goals. The ACC may need the PFC activity to allow it to tell a correct response from an error. Gehring and Knight also found that patients were not as good at correcting their errors compared with controls, further evidence that the PFC is involved in adjusting behavior based on error information.

In addition to the lateral PFC, several other brain regions have been implicated in error monitoring. Falkenstein et al. (2001) found a reduced ERN in patients with Parkinson's disease, indicating that the basal ganglia may also be involved self-monitoring. Obsessive compulsive disorder patients, who may have an overactivity of the basal ganglia, show an increased ERN (Gehring, Himle, & Nisenson, 2000). Lawrence (2000) has argued for an involvement of the basal ganglia in error correction based on his studies with Huntington's Disease patients who have difficulty correcting their motor behavior mid-stream.

Besides these observations, there is not much evidence to suggest what kind of a role the basal ganglia might be playing within the circuitry for error detection. It may be that this region, along with the ACC, is important for integrating motor information with emotional information concerning reward and punishment. An event-related fMRI study by Pagnoni et al. (2002) found activity in the ventral striatum when subjects expected a reward but did not receive one.. In a PET study of feedback processing, Elliot, Frith, & Dolan (1997) found activation in the ventral striatum when subjects received visual feedback in modified Tower of London task. Thus this region may be part of the neural machinery for predicting the outcome of motor actions and comparing them with sensory consequences. Anatomically speaking, the anterior cingulate and ventral striatum are connected via one of many "loops" connecting the frontal cortex to the basal ganglia (Jahanshahi & Frith, 1998). These loops connect the frontal cortex to the basal ganglia, with reciprocal connections back to the frontal cortex through the thalamus. Jahanshahi & Frith (1998) have suggested that this frontostriatal system is particularly important for "willed action", that is, action that is flexible and internally guided, like that expected from the Supervisory Attentional System. This cognitive flexibility that may involve frontostriatal networks is essential to an appropriate response to feedback, where performance must be continually adjusted based on sensory signals.

SENSORY MONITORING AND FORWARD MODELS

Most of the strategies for error detection discussed so far involved monitoring in the motor system to check if the executed action was correct. However, monitoring may also take place by comparing sensory information with a representation of predicted sensory consequences of action. In this form of monitoring the motor efference copy is used to generate a prediction about what will happen as a result of the executed action, a strategy known as "forward modeling" (Blakemore, Rees, & Frith, 1998; Frith, Blakemore, & Wolpert, 2000; Wolpert, 1997). This prediction is then compared with actual sensory results to gauge success.

There is growing evidence that the cerebellum is crucial for generating such predictions (Miall, Reckess, & Imamizu, 2001; Ramnani, Toni, Josephs, Ashburner, & Passingham, 2000; Wolpert, Miall, & Kawato, 1998). Blakemore, Frith, & Wolpert (2001) used PET to investigate the neural mechanisms involved in making sensory predictions about self-generated actions. In this study, subjects controlled a robotic arm with their right hand. This robotic arm made contact with the subject's left hand. In one condition, the movements of the robotic arm were directly responsive to the subject's movements such that the tactile stimulation on the left hand was easily predictable. When a delay was added to the movement of the robotic arm, activity was seen in the right lateral cerebellar cortex, correlated with increasing delays.

The cerebellum may directly interact with somatosensory cortex in the parietal lobe to attenuate sensory signals that are predicted by its forward modeling. Generally, people are more sensitive to unexpected stimuli (Frith et al., 2000), and may not even notice considerable deviations in their movements as long as their expected goal is achieved (Fourneret & Jeannerod, 1998). This may explain why we are not able to tickle ourselves: self-produced sensations are rated as less "tickly" than those produced by someone else. (Blakemore, Frith, & Wolpert, 1999). Blakemore, Wolpert, & Frith (1998) found decreased activation in parietal somatosensory cortex when the stimulation was self-produced compared with when it was externally produced.

Damage to the parietal lobe often produces a self-monitoring deficit known as anosognosia. Anosognosia is an unawareness of deficit, in which the patient denies the existence of a cognitive or behavioral deficit (Bisiach & Geminiani, 1991). The most common form of anosognosia is anosognosia for hemiplegia, in which the patient is paralyzed on one side of the body, but refuses to acknowledge the paralysis. In an illustrative example, Ramachandran (1995) had one patient watch herself in the mirror while he instructed her to move her left arm. Seeing her arm motionless at her side did not change her claim that she had lifted it. In extreme cases, AHP is accompanied by a symptom called somatoparaphrenia, in which the patient actually denies ownership of the limb. Anosognosia occurs most often with right hemisphere damage (Breier et al., 1995), it can be dissociated from unilateral neglect, and does not seem to simply reflect psychological denial on the part of the patient (Bisiach & Geminiani, 1991).

Several researchers have proposed that anosognosia reflects a deficit in comparing sensory feedback with intended goals (Goldberg & Barr, 1991; Ramachandran, 1995; Ramachandran & Rogers-Ramachandran, 1996). Parietal interactions with the cerebellum support this theory. Frith, Blakemore, & Wolpert (2000) suggest that anosognosics fail to successfully compare predicted sensory consequences with the actual sensory results of their actions. Thus, they do not realize the discrepancy between their attempt to move and the lack of movement due to paralysis. If no discrepancy is detected, success may be assumed.

These sensory monitoring mechanisms may be especially important in the case of explicit monitoring, where error feedback is provided to the senses. If positive feedback is the expected result of an action, a negative feedback stimulus would conflict with sensory predictions. This system may then play a significant role in sensory feedback processing.

HEMISPHERIC SPECIALIZATION

A main concern of this dissertation is the hemispheric specialization for executive function. There is little research explicitly focused on this issue, but there is plenty of relevant data. The Error-Related Negativity arises from structures that are so medial that laterality cannot be discerned from ERP data. There is, however, reason to believe that the ACC monitoring system is not completely symmetrical.

First, there are anatomical asymmetries in the anterior cingulate region. The right and left sides of the medial surface of the frontal lobes tend to have different patterns of sulci; the anterior cingulate sulcus is sometimes doubled, with a paracingulate sulcus running in parallel. This double kind of sulcus is more common on the left side than on the right (Ide et al., 1999; Yücel et al., 2001). It has been suggested that this asymmetry may have to do with the paracingulate's involvement in speech (Paus, 2001), but the sulcal patterns do not correlate with similar hemispheric differences in Broca's area (Ide et al., 1999). The right anterior cingulate has a greater volume of gray matter than the left according to a computerized voxel-based analysis of MRI scans (Watkins et al., 2001). There is also a greater surface area on the right anterior cingulate sulcus. Pujol et al. (2002) found that 83% of subjects studies showed a hemispheric asymmetry in the anterior cingulate. Women were more likely than men to show the right sided asymmetry. Insofar as these morphological differences relate to functional differences, they suggest that the left and right systems are not identical. In fact, Pujol et al (2002) did find correlations between the size of the anterior cingulate cortex and behavioral measures of "anticipatory worry", "fear of uncertainty", "shyness with strangers" and "fatiguability". In addition to the anterior cingulate, the entire frontal lobe appears to be larger on the right side (Watkins et al., 2001; Weinberger, Luchins, Morihisa, & Wyatt, 1982).

Neuroimaging research has also produced lateralized results. In an event-related fMRI study of error processing, Kiehl, Liddle, & Hopfinger (2000) found anterior cingulate activity bilaterally and left lateral prefrontal activity associated with errors in a go/no-go task. Menon et al. (2001) also used fMRI to measure error-related neural activity in a go/no-go task, but found activation in the right anterior cingulate, and the insular cortex bilaterally. While these studies did not find identical patterns of activation, they both found error related activity to be partially lateralized. However, there is no consistent pattern of laterality that can be easily interpreted to form a model of hemispheric differences in monitoring based on this data.

Zaidel (1987) has argued for distinct error processing modules in the two hemispheres based in part on evidence from the lexical decision task. In lexical decision, participants must decide whether a string of letters is a real English word or not. Lateralized versions of this task usually fit a "direct access" model, meaning that each stimulus is processed by the hemisphere that receives it directly (Zaidel et al., 1990) thus making it a suitable task to investigate each hemisphere's role in error monitoring. Stein and Zaidel (1987) administered a version of this task in which participants were encouraged to correct their errors by a reward system. The results showed that the pattern of error correction responses was markedly different than that of initial responses. Whereas initial responses showed the typical lexical decision pattern of a right visual field (RVF) advantage, and faster responses to words than to nonwords, the error correction responses showed no visual field advantage, and faster responses to nonwords. The different characteristics of error correction responses were interpreted as evidence that error correction is performed by a distinct error correction module rather than by recomputation in the system that made the initial decision. Furthermore, error correction also appeared to fit the direct access model, which means that each hemisphere was able to independently monitor errors. Error correction was performed equally well by both hemispheres overall, but the right hemisphere showed an early monitoring advantage that decreased with practice, while the left hemisphere's monitoring performance increased with practice. Stein and Zaidel (1987) suggest that this initial right hemisphere superiority in error correction may be due to a general advantage in processing feedback about the external environment.

Iacoboni, Rayman, and Zaidel (1997) made a similar suggestion based on their analysis of how the previous trial affects the current trial in a lateralized lexical decision task. In this experiment, accuracy improved on LVF trials following errors, while performance on RVF trials following errors was unaffected. An improvement after error may be interpreted as an appropriate compensatory response, reflecting a shift in strategy, allocation of resources, or some other adjustment towards better performance. Thus, the increase in accuracy in the LVF following errors may reflect a right hemisphere error processing advantage in lexical decision.

Derryberry (1989) used positive and negative feedback presented both centrally and laterally in a lateralized simple reaction time task in order to examine the effects of different emotional states as feedback for the hemispheres. Positive feedback was provided after fast trials, and negative feedback was provided after trials that were inaccurate or slow. By manipulating the reaction time criteria for positive feedback, Derryberry created some blocks containing mostly negative feedback, and others with mostly positive feedback. Experiments 1 and 2 used feedback presented centrally. The main result was that in mostly negative feedback blocks, reaction time was faster to right visual field (RVF) targets, while in mostly positive feedback blocks reaction time was faster to left visual field (LVF) targets. Comparing these conditions to a control in which no feedback was presented led to the interpretation that negative emotion interferes with right hemisphere (RH) performance, while positive emotion facilitates RH performance. Experiment 3 replicated these results with lateralized feedback stimuli. In this experiment, the feedback stimuli were letter grades, with 'A' serving as positive feedback,' C' as neutral feedback, and 'F' as negative feedback. Reaction time analysis showed that responses were faster in the LVF after positive feedback, and faster in the RVF after negative feedback, with no difference occurring after neutral feedback. Thus, positive feedback shifted performance in favor of the RH, while negative feedback shifted performance in favor of the LH.

Manipulations of the time between the feedback signal and the target stimulus showed that the feedback effects were greatest at 500 ms SOAs and less at 250 or 740 ms

SOAs. Derryberry interpreted these results as indicating a "phasic arousal" mechanism activated by the right hemisphere. There is extensive evidence that the right hemisphere is sensitive to emotional processing and may control arousal mechanisms (Davidson, 1995, Tucker & Williamson, 1984). Tucker & Williamson (1984) have proposed more specifically that the RH responds in opposite ways to positive and negative emotions. According to Tucker & Williamson, right frontal regions become activated in negative mood states and serve to inhibit posterior perceptual regions of the brain, while positive moods decrease activity in the right frontal lobe leading to less inhibition. Derryberry considers the feedback in his experiments to elicit emotional responses, and suggests that the RH role in emotional control may account for his results.

Derryberry (1990) further explored the mechanism of this feedback effect by manipulating stimulus-response compatibility. The aim was to specify the locus of this emotional interference. The reasoning goes that if the interference is perceptual, then manipulating stimulus-response mappings should not interact with feedback effects. However, if the interference affects the RH at motor or pre-motor level then this manipulation should interact with the feedback effects. There were 3 experiments in this paper that all used the same computer-based reaction time task with letters as feedback. Results showed that spatial compatibility did indeed interact with the feedback effects. Derryberry interprets these findings to "provide additional evidence that feedback-related emotional states modulate information processing within the right hemisphere" (p. 1268). These data are also used to form a more sophisticated interpretation of the feedback mechanism. Derryberry reasons, in line with Tucker & Williamson, that the negative feedback leads to increased right frontal activity. However, in contrast with Tucker & Williamson, he claims that the resulting inhibition from the frontal lobe affects the communication between perceptual and motor systems, thus explaining the interaction with S-R compatibility in his results.

There are, however, alternate interpretations of these results. It is not clear that an "emotional" state was elicited by the feedback stimuli. Derryberry refers to the emotion resulting from negative feedback as frustration, but this state does not fall obviously along the positive-negative mood axis the right hemisphere has been associated with. Secondly, the nature of the feedback signals must be considered. The letters "A" and "F" are used to indicate good and poor performance respectively, and "C" is used as a middle baseline. Feedback with the letter "C" may not be an appropriate baseline. The subjects in these experiments were college students to whom a "C" may represent unsatisfactory performance. Moreover, in this task if subjects are striving to respond as quickly as possible, a "C" may indicate failure to achieve the fastest category. Thus, the axis that has been interpreted as corresponding to positive-negative emotion may instead reflect increasing error awareness. In this view, reaction times following positive feedback may be considered a baseline in which no error has been detected. Then, the slowing of RH reaction times following "C" and "F" feedback may be interpreted as reflecting increased failure-related processing. Our experiments generally use a content-neutral stimulus as a control to insure there is no success or failure related processing .

Other experiments that have investigated hemispheric responses to feedback have similar interpretational difficulties. Kostandov (1988) used three different types of feedback in a lateralized task that required participants to distinguish time intervals between stimuli. Unfortunately, participants always used the left hand to respond that the interval was short and the right hand to indicate that it was long, which makes it difficult to draw conclusions about each hemisphere's role in processing the feedback.

A suggestion about hemispheric specialization for monitoring comes from the literature on anosognosia, the unawareness of deficit resulting from injury to the parietal lobes. Anosognosia occurs most often with right hemisphere damage (Bisiach & Geminiani, 1991). The right parietal lobe may be specially involved in sensory monitoring (Goldberg & Barr, 1991; Ramachandran, 1995; Ramachandran & Rogers-Ramachandran, 1996). Ramachandran (1995) proposes that the two hemispheres have different ways of dealing with detected discrepancies. The left hemisphere tends to explain away apparent contradictory evidence. It creates a "story" to account for why an observed result does not match internal intentions. The right hemisphere, however, has a general purpose "anomaly detector" that is concerned with perceiving anomalies and causing changes in behavior. For example, if both hemispheres notice that the left arm is not moving, normally the right hemisphere will sound an alarm and let the left hemisphere know that the arm did not move. If the right hemisphere is damaged, though, the left hemisphere will confabulate a reason for the inaction. According to Ramachandran, when an anomaly is detected, the left hemisphere "tries to impose consistency by ignoring or suppressing the contrary evidence" whereas the right hemisphere "forces a complete change in one's world view - a paradigm shift." (p. 40) A similar version of this hypothesis was originally proposed by D. Zaidel (1994).

The right hemisphere has also recently been implicated in several processes related to self-concept, which relates directly to its role as a self-monitor (Keenan et al., 1999). In one experiment, participants were asked to decide if each of list of adjectives described themselves, or, in another condition, if the adjective described a friend. Applying transcranial magnetic stimulation to the right frontal cortex slowed down self judgements, but not judgements about a friend. Stimulation of the left side had no effect (Keenan, 2000).

However, evidence for a right hemisphere superiority in error monitoring is rather weak at this point. The evidence from the lexical decision task is suggestive, but there are many questions. The first several experiments in this dissertation specifically tested the ability of each hemisphere to respond to performance feedback in the lexical decision task. The experimental paradigm involves presenting accuracy feedback after every trial, lateralized to the right visual field (RVF) or to the left visual field (LVF). In different blocks subjects receive feedback either in one visual field, in both, or in neither. This allows the measurement of behavioral responses to feedback information that is processed initially by one or the other hemisphere of the brain. In this case, we are focusing on explicit monitoring, that is, how the hemisphere responds to explicit information about the correctness of a response. However, in blocks where no feedback is presented we can also measure implicit monitoring, the extent to which the subjects respond to their errors in the absence of feedback. The blocked design allows examination of the immediate effects of feedback on the subsequent trial, as well as the long-term effects across blocks of trials. Based on results from these experiments it will be argued that the right hemisphere is indeed a better self-monitor in this task. Several additional experiments explore the possibility that each hemisphere may be sensitive to different types of feedback information.

An important issue in understanding how monitoring functions are split across the two hemispheres involves how different types of cognitive operations are monitored. To what extent does the right hemisphere monitoring advantage extend to other cognitive domains? Evidence from a visuo-spatial task will suggest that monitoring functions may be dynamically allocated depending on hemispheric specialization for the current task. That is, in a right hemisphere task the left may take over monitoring functions.

The case of the split brain, in which the two hemispheres are surgically separated, allows for the testing of each hemisphere's monitoring functions separately. I will report the results of an experiment in which a split-brain patient was required to detect errors with either the left or right hemisphere.

Finally, a functional MRI study was conducted to measure brain activity associated with lateralized feedback processing in lexical decision. Examination of neural regions that are active when feedback is present or absent will elucidate the relationship of hemispheric processing to the networks for self-monitoring I have described above.

Experiment 1: **Lateralized feedback in lexical decision.**

The goal of this experiment was to test each hemisphere's response to performance feedback. Since feedback is given explicitly, this experiment really tests the ability of each hemisphere to utilize error information to guide performance. The lateralized lexical decision task was chosen because it is task that both hemispheres are capable of performing (Measso & Zaidel, 1990). In lexical decision, the participant must decide of a string of letters forms a real English word or not. We used a bilateral version of the lexical decision task, where a target stimulus is presented in one visual field and a distractor is presented in the other. This condition has been shown to increase hemispheric independence compared to the unilateral task (Iacoboni & Zaidel, 1996). The procedure involves presenting a feedback stimulus in the form of a woman's face after each trial: the face was smiling to indicate a correct response and frowning to indicate an error.

A typical pattern of results in a lateralized lexical decision task involves a RVF advantage in which subjects respond more quickly and accurately to RVF stimuli. Additionally, subjects are typically faster at responding to words than to nonwords, and this difference tends to be greater in the RVF (Iacoboni et al., 1997; Iacoboni & Zaidel, 1996; Measso & Zaidel, 1990). Based upon the results of the Stein & Zaidel (1987) error correction study, and the previous trial effect found by Iacoboni, Rayman, & Zaidel (Iacoboni et al., 1997) , we predicted that the right hemisphere would be better than the left at using performance feedback.

METHOD

Participants. Twelve male and twelve female students participated in this experiment for partial course credit. Participants learned English as their first language, had normal or corrected-to-normal vision, and were strongly right-handed as determined by a handedness questionnaire (Oldfield, 1971).

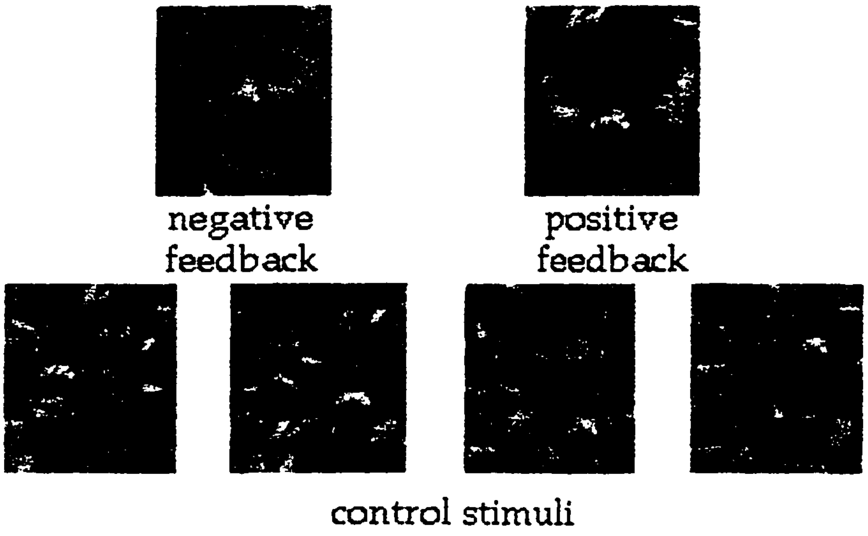
Materials and Apparatus. Two lists of 3, 4, and 5 letter strings were created, each consisting of 64 English words and 64 pronounceable nonwords. Words were counterbalanced for spelling-sound regularity and for frequency in the language. For each participant, each list was randomized and strings from one list were paired with strings of equal length from the other list to create 128 trials each with a target and distractor. Thus, one list served as the LVF stimuli and the other served as the RVF stimuli. Which list was presented to which visual field was counterbalanced across participants. Items that occurred as targets in one block served as distractors in the other block.

Participants sat with their chin in a chinrest so that their eyes were 57.3 cm from a computer monitor controlled by an Apple IIsi computer. Their hands were positioned so that the middle and index fingers of both hands rested on switches on a response box positioned at midline, with palms facing each other. The switches were aligned vertically so that the index fingers rested on the two top switches and the middle fingers rested on the two bottom switches. Stimuli were presented using the MacProbe software developed by Dr. Steven Hunt.

Procedure Eight of the participants (four male, four female) were randomly assigned to the control ("no-feedback") condition; the other sixteen served in the experimental ("feedback") condition. A fixation cross remained at the center of the screen throughout the experiment and participants were instructed to keep their eyes focused on it at all times. Letter strings were presented in lower-case black letters on a gray background for 150 ms. On each trial, one string was presented to the left of fixation and one to the right of fixation, with the more central edge of each stimulus at 1.5° of visual angle from fixation. The strings were printed in 24 point bold Helvetica font. One of the letter strings was underlined, indicating the target. On half of the trials, the target was in the RVF and in the other half the target was in the LVF. The participant was instructed to respond to the underlined string by pressing both of the top switches to indicate it was a word and both of the bottom switches to indicate a nonword. Thus, the responses were made bimanually.

Each participant received 24 practice trials, then completed two blocks of 128 trials each. Participants in the feedback condition completed one block in which feedback was presented only to the RVF and one block in which feedback was presented only to the LVF. The order of these blocks was counterbalanced across participants. Feedback was only presented in the visual field where the target letter string had just been. For example, in a LVF-feedback block, participants would receive feedback in the LVF after each trial in which the target was in the LVF, and would receive a meaningless control stimulus in the RVF on each trial in which the target was in the RVF. The feedback was presented 225 ms after the response and remained on the screen for 150 ms. The feedback stimulus consisted of a digitized grayscale photograph of woman's face. The pictures subtended 2.3° of visual angle in width and 2.7° in height, with the innermost edge at 1.5° from fixation. The face was smiling if the response just made was accurate, and frowning if the response just made was inaccurate. Several control stimuli were created by scrambling the frowning and happy pictures so that they were unrecognizable. Control participants were presented with a scrambled picture after every trial. The stimuli are presented in Figure 4.

Figure 4: Feedback stimuli for Experiment 1



RESULTS

Lexical decision variables. The data for the control participants were submitted to a 2 (visual field of target: left, right) X 2 (wordness of target: word, nonword) repeated measures ANOVA for both latency and percent error. All three of the expected findings were significant. There was better performance in the RVF (14.9% errors, 765 ms) compared with the LVF (24.4% errors, 790 ms) ($F(1, 7) = 5.75, p < .05$ for latency and $F(1, 7) = 14.1, p < .01$ for percent error). There was a wordness advantage, with 16.2% errors and 712 ms mean reaction time for word targets and 23% errors and 835 ms mean reaction time to nonword targets ($F(1, 7) = 19, p < .01$ for latency, not significant for percent error). There was also a significant interaction between wordness and visual field ($F(1, 7) = 13.86, p < .01$ for latency and $F(1, 7)=5.66, p < .05$ for percent error). This interaction fit the standard pattern, where RVF words responses showed better performance (8.6% errors, 680 ms) than RVF nonword responses (21.1% errors, 833 ms), while there was a smaller difference between LVF word responses (23.8% errors, 744 ms) and LVF nonword responses (25% errors, 837 ms). Thus, there seem to be no effects of a meaningless visual stimulus after each trial.

Explicit monitoring. Two analyses were performed on the feedback group data. The first looked at the global effects of feedback across blocks. We performed a comparison of the left and right visual field feedback blocks with a 2 (visual field of target: left, right) X 2 (wordness: word, nonword) X 2 (feedback block: LVF feedback, RVF feedback) ANOVA for both percent error and latency data. The three usual findings were again significant in these data: better performance in the RVF (20.2% errors, 731 ms) compared with the LVF (30% errors, 756 ms) ($F(1, 15) = 9.34, p < .01$ for latency and $F(1, 15) = 22.03, p < .001$ for percent error), better performance for word targets (22.2% errors, 712 ms) compared with nonword targets (28.1% errors, 775 ms)

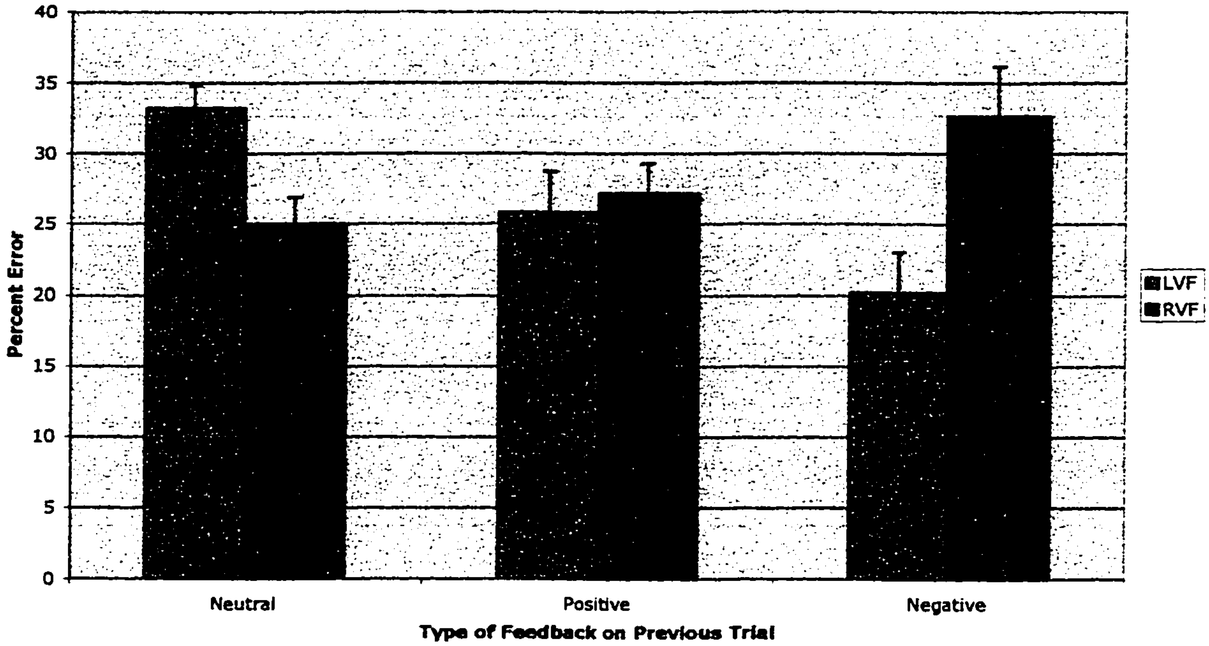
($F(1, 15) = 95.71, p < .001$ for latency and $F(1, 15) = 5.83, p < .05$ for percent error) and a wordness X visual field interaction ($F(1, 15) = 22.14, p < .001$ for latency, and $F(1, 15) = 7.87, p < .05$ for percent error). Interestingly, there was a main effect of feedback block on percent error ($F(1, 15) = 6.30, p < .05$), with participants responding with fewer errors in the LVF feedback blocks (23.6%) than in RVF feedback blocks (26.6%). Feedback block interacted with visual field of target in both percent error ($F(1, 15) = 14.42, p < .005$) and latency ($F(1, 15) = 39.13, p < .001$). In LVF feedback blocks, participants were faster responding to LVF targets (741 ms) than to RVF targets (751 ms), while in the RVF feedback blocks participants responded faster to RVF targets (711 ms) than to LVF targets (769 ms). According to planned comparisons, only the RVF feedback difference was significant ($F(1, 15) = 56.807, p < .001$). Percent error also shifted in favor of the visual field that was receiving feedback. In the RVF feedback condition, there was a large difference between LVF targets (34.4%) and RVF targets (18.8%). Planned comparisons revealed that this difference was significant ($F(1, 15) = 53.45, p < .001$). In the LVF feedback condition, however, there was no significant difference between LVF and RVF error rates.

There was also a three-way interaction between wordness, feedback block, and visual field of target for latency ($F(1, 15) = 46.06, p < .001$). This interaction was due to a normal wordness X visual field interaction in the RVF feedback blocks, with words (657 ms) faster than nonwords (765 ms) only in the RVF, but a different pattern in the LVF feedback blocks. In the LVF feedback blocks LVF word responses (708 ms) were faster than LVF nonwords responses (775 ms) ($F(1, 15) = 89.45, p < .001$) *and* RVF word responses (714 ms) were faster than RVF nonword responses (789 ms) ($F(1, 15) = 111.03, p < .001$).

The second analysis looked at the effect that positive and negative feedback had on the subsequent trial. Data were analyzed in a 3 (type of feedback on previous trial: none, positive, negative) X 2 (feedback block: LVF feedback, RVF feedback) repeated measures ANOVA. There was a main effect of feedback block for percent error ($F(1, 15) = 13.247, p < .01$). Responses were more accurate in LVF feedback blocks (23.1% errors) than in RVF feedback blocks (28.3% errors). There was no main effect of feedback type, but there was an interaction between feedback type and block for percent error ($F(2, 30) = 5.90, p < .01$) (see Figure 5).

Planned comparisons motivated by our error-monitoring hypotheses examined error rates following negative feedback trials. Error rate following negative feedback presented in the LVF (20.2%) was significantly lower than after positive feedback presented in the LVF (25.8%) ($F(1, 30) = 4.720, p < .05$). Error rate following feedback presented in the RVF, however, was actually higher after negative (32.6%) compared to positive (27.2%) feedback, although this difference was not significant.

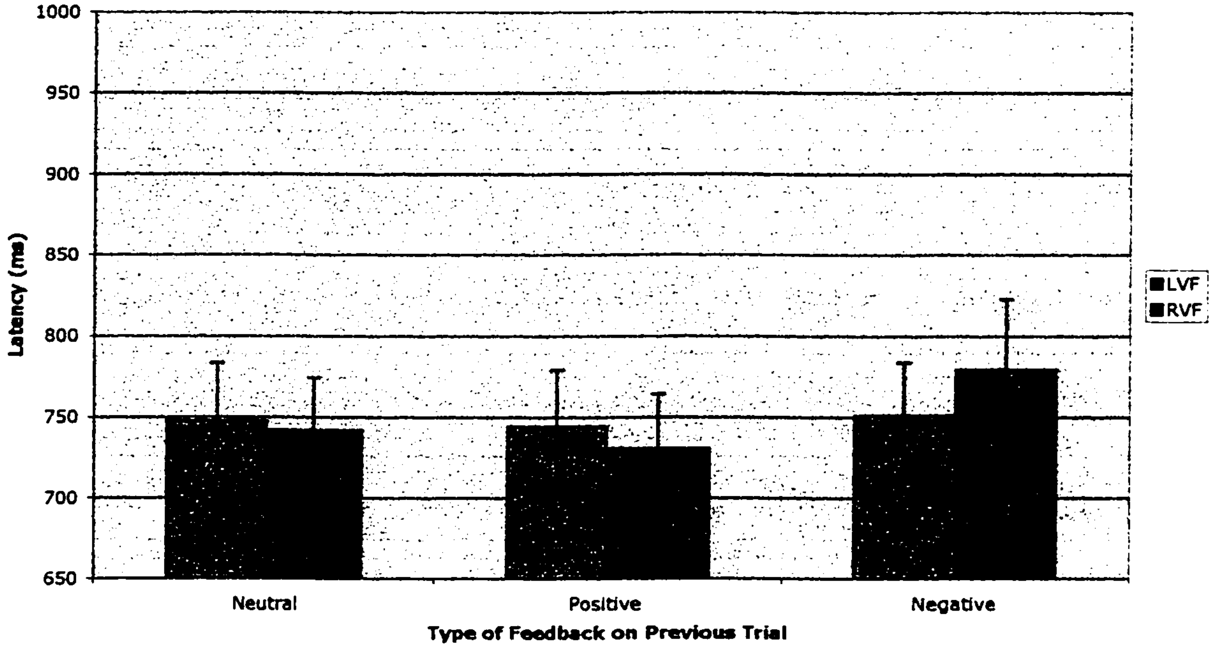
Figure 5: Interaction between previous trial feedback type and feedback block for Experiment 1



Analysis of the latency data showed no significant main effect of block, and no main effect of previous trial feedback type. These data are shown in Figure 6. There was no significant interaction between the two variables, but planned comparisons were performed in order to examine the effects of feedback within each visual field since these effects were of theoretical interest. These comparisons were motivated by our expectation that trials following negative feedback would reflect error monitoring processes. The comparisons revealed that reaction time following negative feedback presented in the RVF (779 ms) was slower (F (1, 30) = 5.20, $p < .05$) compared with trials following no feedback in the RVF (742 ms). Latency following positive RVF feedback trials was not significantly different (731 ms) from the no feedback condition. There were no effects of feedback type on latency when feedback was presented to the

LVF, thus there is no evidence that the increase in accuracy following negative feedback to the LVF is due to a speed-accuracy tradeoff.

Figure 6: Interaction between previous trial feedback type and feedback block for Experiment 1



Implicit monitoring. This analysis involves the control blocks in which no meaningful feedback was given. Is there a similar pattern of results after errors even when no feedback is given? We analyzed the control blocks with a 2 (correctness of previous trial: correct, incorrect) X 2 (visual field of previous trial: left, right) X 2 (visual field of present trial: left, right) repeated measures ANOVA for percent error and latency. Participants were not significantly slower on trials following errors (790 ms) than trials following correct responses (783 ms). Nor was there any difference in error rate on trials following errors (19.0%) compared to correct responses (19.7%). Previous trial correctness did not significantly interact with previous trial visual field or present trial visual field, thus we did not find evidence of implicit monitoring.

All analyses were also conducted with sex as a between-subject variable. There was no main effect of sex, and sex did not interact with any other variable in these data.

DISCUSSION

The control participants showed the standard lexical decision pattern, indicating that the presence of a meaningless stimulus after the response did not affect performance. Nor did control participants show any evidence of implicit monitoring; the characteristic slowdown after error trials observed by Rabbitt & Vyas (1970) was not seen here. This may be explained by the presence of the scrambled control stimulus after each trial. This intertrial distraction served to space the trials temporally as compared to most serial reaction time tasks. Also, whatever minimal processing of the scrambled picture took place may have masked any error-related slowing.

Adding meaningful feedback to the task changed the pattern of performance. Participants made fewer errors and responded faster in the visual field that was receiving the feedback. This result is not surprising; participants often reported being more attentive to the field in which they were receiving feedback information.

The finding that negative feedback presented to the right hemisphere caused an decrease in error rate while the same feedback presented to the left hemisphere increased latency on the following trial provides evidence that feedback is processed independently by each hemisphere. If the feedback information were shuttled across the corpus callosum to a specialized component in one hemisphere regardless of where it was presented, we would expect to see similar patterns in response to negative and positive feedback regardless of where it was presented. Instead we have an almost complete reversal of effect depending on hemifield of presentation.

The differential effects of feedback presented to the two visual fields can be interpreted as indicating a right hemisphere superiority for error monitoring in this task. Feedback to the right hemisphere seems to initiate a more appropriate response; LVF feedback blocks were more accurate overall and negative feedback led to a compensatory response as indicated by the increase in accuracy on the next trial. This result is consistent with Stein and Zaidel's (1987) finding of initial right hemisphere superiority in detecting errors, and with Iacoboni, Rayman, and Zaidel's (1997) previous trial analysis. This interpretation is also consistent with Derryberry's (1989, 1990) finding of right hemisphere sensitivity to feedback, although in his experiments negative feedback presented the RH led to a slowing in reaction times. The lexical decision task in the present experiment may allow for more flexibility in strategy readjustment than Derryberry's simple reaction time task. That task did not allow for measurement of error rate as a dependent variable. A right hemisphere error monitoring advantage is also consistent with the phenomenon of anosognosia, where right parietal damage leads to a monitoring deficit.

If the right hemisphere initiates compensatory mechanisms in response to negative feedback, this may explain the effects on wordness. The pattern following feedback to the left hemisphere was no different from the typical pattern observed in this task; there was a wordness advantage that was greater in the RVF. Presenting feedback to the right hemisphere, however, resulted in an unusual pattern in which the wordness advantage was the same in both visual fields. The altered pattern suggests a shift in strategy initiated by the right hemisphere.

It might be argued, however, that the apparent RH advantage in responding to feedback is due to a superior ability to process faces or facial emotions (Adolphs, Damasio, Tranel, & Damasio, 1996; Nakamura et al., 1999). Experiment 2 uses neutral colored squares instead of faces to address this issue.

Experiment 2. **Feedback with colored squares.**

The purpose of this second experiment was to clarify the results of Experiment 1 by providing a lateralized feedback stimulus that was "hemisphere neutral". The ideal feedback stimulus for this experiment is one that both hemispheres can identify with equal ease. We chose to use square patches of different colors to indicate right and wrong answers. In addition, in contrast to Experiment 1 we used a within-subjects design to allow for better cross-conditional analyses.

METHOD

Participants. A total of 32 UCLA undergraduate students (16 male, 16 female) participated in this study for partial course credit. All participants learned English as their first language and were strongly right-handed as determined by a modified Oldfield-Edinburgh handedness inventory. All had normal or corrected-to-normal vision.

Materials and Apparatus. The chinrest setup, response box, computer, and computer software were identical to those used in Experiment 1. Since this experiment requires participants to complete four blocks of trials, new word lists were created. These word lists were adapted from Iacoboni and Zaidel (1996). Two lists of 96 stimuli pairs were created, counterbalanced for regularity and frequency. Each pair was matched for length, and consisted of 3, 4, 5, and 6 letter strings. Words that were targets in one block became distractors in another to create the four blocks.

positive and negative feedback

neutral feedback

Figure 7: Feedback stimuli for Experiment 2

Procedure. The bilateral lexical decision procedure was the same as for Experiment 1, with two changes. First, the feedback stimuli were replaced with solid colored squares of the same size (2.3° wide by 2.7° high). Three colors were used. A black square served as the control/neutral stimulus. Participants were told that the black square did not provide any information about their performance. A blue square and a yellow square served as the meaningful feedback. These stimuli are depicted in Figure 7. Half of the participants saw a blue square after each correct trial and a yellow square after each incorrect trial. The colors were reversed for the other half of the participants. The second change was that after a practice block of 24 trials, each participant completed four blocks of 96 trials each. One block was a control in which a black square appeared after each trial in the same visual field as the target. Thus, in the control block participants did not receive any explicit feedback. Participants also completed a RVF feedback block and a LVF feedback block corresponding to the two experimental conditions in Experiment 1. Again, in RVF feedback blocks colored squares indicating correctness appeared after all RVF targets, while black squares appeared after all LVF targets. In LVF feedback blocks meaningful feedback was presented only after LVF targets, and black squares appeared after all RVF targets. In a fourth block, participants were presented with meaningful feedback after *both* LVF and RVF trials.

RESULTS

All data points that were greater than 3 standard deviations away from the mean of each cell were discarded.

Lexical decision variables. The first analysis looked at the lexical decision pattern across the four blocks with a 2 (visual field of target: left, right) X 2 (wordness: word, nonword) X 4 (feedback block: Control, LVF feedback, RVF feedback, Both) repeated measures ANOVA for both percent error and latency. Once again, we obtained the classic lexical decision pattern. There was a significant right visual field advantage (RVFA) overall, $F(1, 31) = 96.44, p < .0001$, with 17.3% errors in the RVF and 28.9% in the LVF. Participants were also significantly faster when targets were in the RVF (754 ms) as opposed to the LVF (809 ms), $F(1, 31) = 30.98$ $p < .0001$. There was also a wordness advantage in percent error (19% errors for words, 27.1% errors for nonwords, $F(1, 31) = 6.78, p < .05$) and in latency (743 ms for words, 820 ms for nonwords, $F(1, 31) = 84.07, p < .0001$). In addition, we again found an interaction between wordness and visual field in percent error ($F(1, 31) = 22.663, p < .0001$) and latency ($F(1, 31) = 84.56, p < .0001$). There was no main effect of feedback block, and feedback block did not significantly interact with any other variable in the accuracy data. However, in the latency data, feedback block interacted with visual field ($F(3, 93) = 6.16, p < .001$) and with wordness ($F(3, 93) = 3.84, p < .05$).

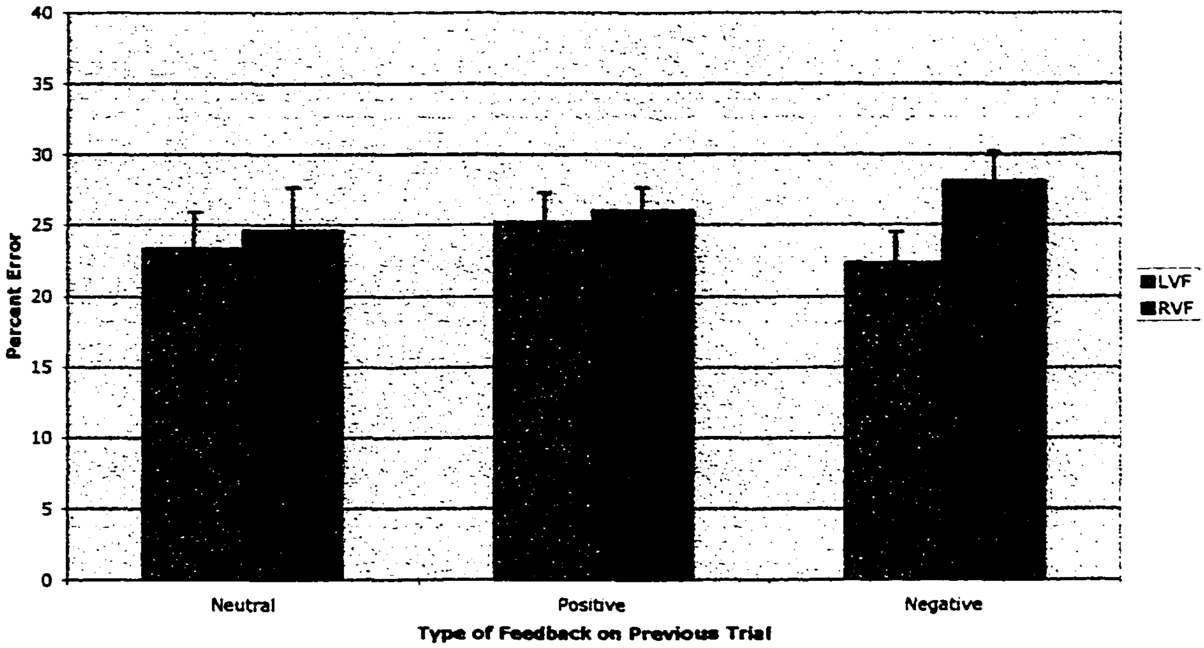
A series of post-hoc comparisons using the Bonferonni correction was used to examine these interactions. The interaction between visual field and feedback block showed the same pattern as in Experiment 1, where reaction times were slower in the visual field not receiving feedback. Thus, in the RVF feedback blocks, LVF trials were significantly slower (827 ms) than LVF trials in the control block (793 ms), $F(1, 93) = 17.26, p < .001$, while RVF trials (745 ms) were not significantly slower compared with control blocks (739 ms). In the LVF feedback blocks, RVF trials (773 ms) were slower than RVF trials in control blocks (739 ms), $F(1, 93) = 17.11, p < .001$, whereas LVF trials (806 ms) were not significantly slower compared to the control blocks (793 ms). There was no significant slowdown in either visual field in the "Both" blocks. Analysis of the wordness x block interaction revealed that the presence of feedback in a block slowed down the processing of words, but not of nonwords. Each of the three feedback blocks showed significantly slower reaction time to word targets as compared with the 716 ms mean reaction time for words in control blocks (LVF feedback blocks:

749 ms, $F(1, 93) = 13.52, p < .001$, RVF feedback blocks: 755 ms, $F(1, 93) = 18.66, p < .001$, "Both" blocks: 751 ms, $F(1, 93) = 15.03, p < .001$). None of the three blocks showed a significant difference in reaction time to nonword targets as compared with control blocks.

Explicit monitoring. The second set of analyses looked at the effect of feedback on the following trial. The LVF feedback blocks and RVF feedback blocks contained trials with all three types of feedback (positive, negative, and neutral) whereas the "Both" blocks did not contain any trials with neutral feedback. For this reason, we analyzed the "Both" blocks separately. A 2 (feedback block: LVF feedback, RVF feedback) X 3 (type of feedback on previous trial: none, positive, negative) repeated measures ANOVA was conducted on the error and latency data from the LVF and RVF feedback blocks. One participant did not have any valid trials in one of the cells due to a small number of errors in the RVF feedback block and was not included in this analysis.

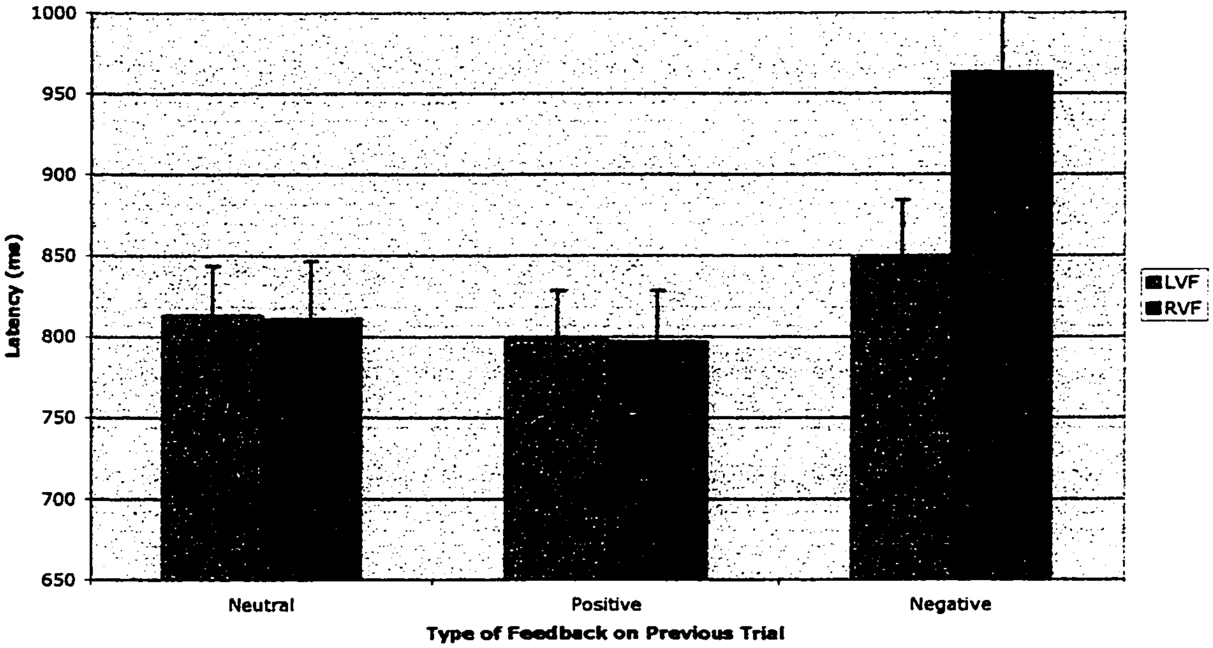
The error data are shown in Figure 8. In the error data, there was no significant main effect of block or of previous trial feedback type. Also, although the pattern looks remarkably similar to the one obtained in Experiment 1, the interaction between feedback block and previous trial feedback type was not significant. Motivated by the results of Experiment 1, we looked at the trials following negative feedback with a planned comparison, and found that participants made significantly fewer errors when the negative feedback had been presented to the LVF (22.3%) as opposed to the RVF (28.1%), $F(1, 60) = 5.789, p < .02$. The latency data, which are shown in Figure 9, showed no significant main effect of feedback block, but there was a significant main effect of previous trial feedback type, $F\,(2, 60)=4.188$, $p < .02$. This reflected an error-related slowdown such that trials following negative feedback (906 ms) were about 100 ms slower than trials following positive (798 ms) or neutral (812 ms) feedback. There was no significant interaction between feedback block and previous trial feedback type, but there is some evidence that the error-related slowdown was greater when negative feedback was presented to the RVF. A planned comparison revealed a marginally significant difference between response times following negative feedback presented to the RVF (963 ms) compared to those following negative feedback presented to the LVF (848 ms), $F\,(1, 60) = 3.74$, $p < .06$. Thus, as in Experiment 1, negative feedback presented to the RVF tends to slow down and *decrease* accuracy on subsequent trials, whereas negative feedback presented to the LVF tends to slow down and *increase* accuracy on subsequent trials.

Figure 8: Interaction between previous trial feedback type and feedback block for Experiment 2



The "Both" blocks were then analyzed with a 2 (type of feedback on previous trial: positive, negative) X 2 (visual field of previous trial: left, right) repeated measures ANOVA for percent error and for latency. The error data revealed no main effect of type of feedback or of visual field, but a significant interaction between the two, $F(1, 31) = 4.58, p < .05$. A planned comparison shows that there is a significant difference between error rate following LVF negative feedback as compared to RVF negative feedback, $F(1, 31) = 6.923, p < .05$. This result is in the opposite direction as that found in the other blocks, with errors following RVF negative feedback less frequent (20.5%) than following LVF negative feedback (25.3%). The latency data showed a main effect of previous trial feedback type, $F(1, 31) = 14.36, p < .001$, reflecting slower responses after negative feedback (853 ms) compared to positive feedback (787 ms). There were no further significant effects or interactions.

Figure 9: Interaction between previous trial feedback type and feedback block in Experiment 2



Implicit monitoring. To test for implicit monitoring, we subjected the error rate and latency data from the control blocks to a 2 (correctness of previous trial: correct, incorrect) X 2 (visual field of previous trial: left, right) repeated measures ANOVA. No significant results were found for either error or latency data. We also repeated this analysis using current trial visual field as the second variable and still found no significant effects.

All analyses were also conducted with sex as a between-subject variable. There was no main effect of sex, and sex did not interact with any other variable in these data.

DISCUSSION

The effect of colored squares as feedback in Experiment 2 was similar to the effect of the faces in Experiment 1. When negative feedback is presented to the RVF, performance is worse on the following trial compared to when negative feedback is presented to the LVF. Participants show a greater slowdown and increased error rate following negative feedback presented to the RVF or left hemisphere. It appears that this effect is dependent on the presence of the feedback stimulus itself, since we obtained no evidence of implicit monitoring.

We may learn something about the locus of the feedback effect from these data. In comparison to the control blocks, reaction times to word targets was slower in the three feedback blocks. Nonword trials were not any slower in the feedback blocks. This suggests that the presence of feedback may initiate a shift in strategy that affects word processing but not nonword processing. This idea also supports the independence of word and nonword processing (Iacoboni & Zaidel, 1996).

There are two important differences between the results of Experiment 1 and 2. First, the interaction between block and type of feedback on previous trial was not significant in the second experiment. The visual field differences in feedback response were more robust when the feedback stimuli were faces as opposed to colored squares. Second, the "Both" blocks did not show the same pattern, indicating that the blocked nature of feedback was essential for the effect. Perhaps the mixed nature of the "Both" blocks clouded the contribution of each hemisphere to error monitoring. This suggests that the error monitors in both hemispheres are not independent of each other.

The attenuated interaction between feedback type and block suggested that the faces may have been a more effective right hemisphere feedback stimulus than the squares. Each hemisphere may be sensitive to different types of feedback. For example, it is possible that the left hemisphere is able to utilize verbal feedback more efficiently than the right. To test this idea, we ran a third experiment using verbal feedback.

Experiment 3. **Feedback with words.**

The hypothesis being developed here is that the mechanisms in each hemisphere that take explicit feedback about performance and use it to adjust behavior are differentially sensitive to certain modes of feedback. The right hemisphere seemed particularly sensitive to facial stimuli. We might expect the left hemisphere to be particularly adept at using verbal information to guide behavior, so this experiment uses words as feedback to test this hypothesis.

METHOD

Participants. For this experiment, 32 different UCLA undergraduate students (16 male, 16 female) participated for partial course credit. All participants learned English as their first language and were strongly right-handed as determined by a modified Oldfield-Edinburgh handedness inventory. All had normal or corrected-to-normal vision.

Materials and Apparatus. The chinrest setup, response box, computer, and computer software were identical to those used in Experiments 1 and 2. The word lists were identical to those used in Experiment 2.

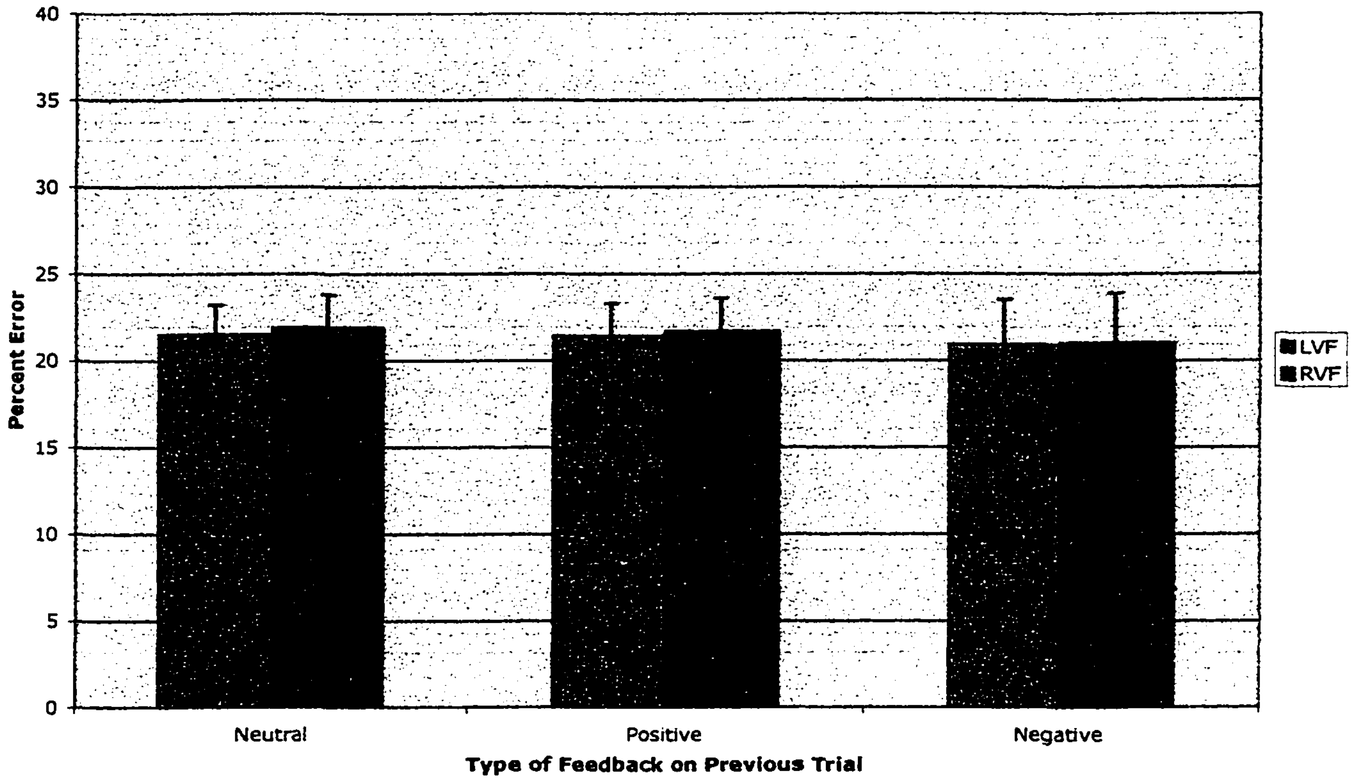
Procedure. The procedure was the same as Experiment 2 except that the feedback stimuli were changed to the words "none" for the control stimulus, "good" for a correct response, and "error" for an incorrect response. These words were chosen because they all appeared approximately the same length on the computer screen. We avoided using the word "right" to indicate a correct response due to its other meaning as the opposite of "left". The feedback stimuli, like the lexical decision targets, were printed in black 24 point bold Helvetica font.

RESULTS

Once again, data points that were greater than 3 standard deviations away from the mean of each cell were discarded.

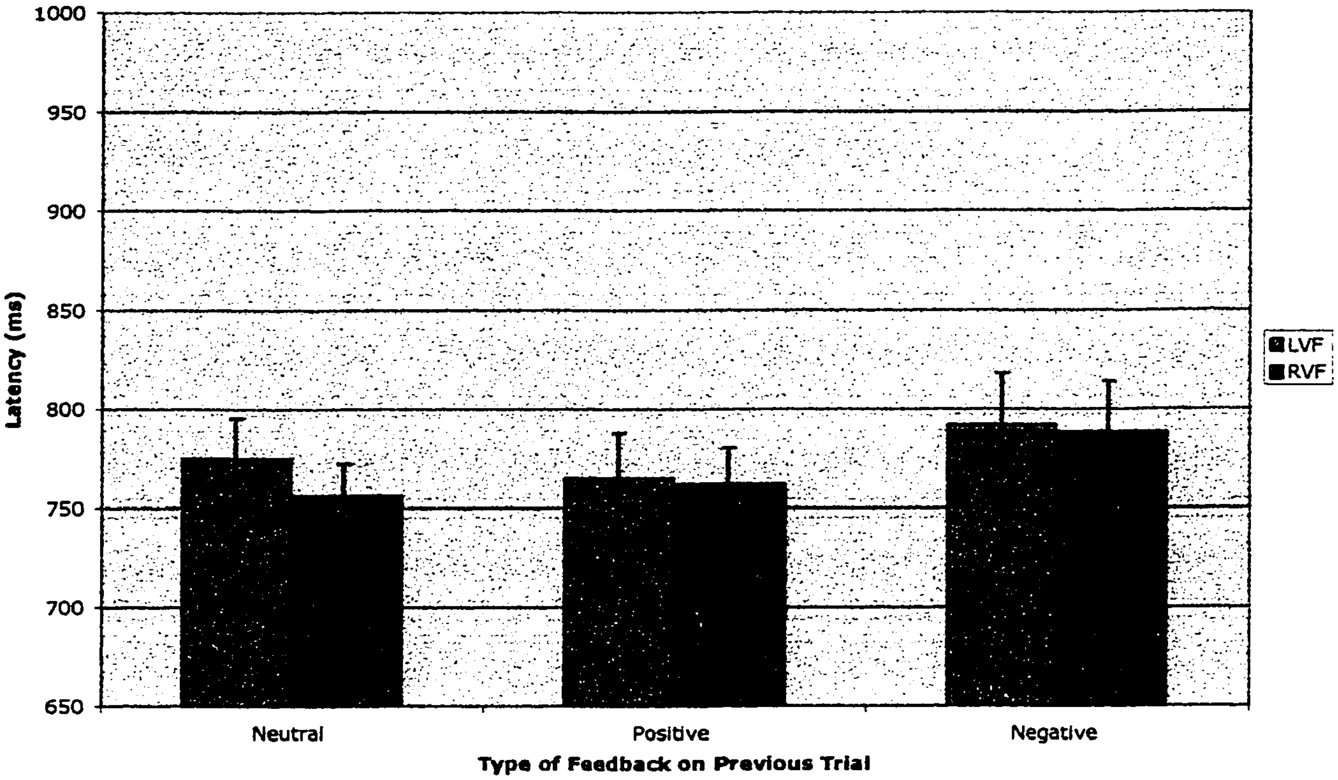
Lexical decision variables. We conducted a 2 (visual field of target: left, right) X 2 (wordness of target: word, nonword) X 4 (feedback block: control, LVF feedback, RVF feedback, Both) repeated measures ANOVA for both percent error and latency data. These data too showed the classic lexical decision pattern. There was a main effect of visual field in percent error, $F(1, 31) = 56.98, p < .0001$, with fewer errors in the RVF (16.1 %) than in the LVF (26.7%). Participants also responded faster to RVF targets (749 ms) than to LVF targets (781), $F(1, 31) = 48.52, p < .0001$. There was a significant main effect of wordness in latency (725 ms for words, 804 ms for nonwords, $F(1, 31) = 48.52, p < .0001$), and a trend towards a wordness advantage in percent error (21.1% errors for words, 22.7% errors for nonwords, $F(1, 31) = 3.50, p < .08$). The wordness by visual field interaction was again significant for percent error ($F(1, 31) = 47.00, p < .0001$) and latency ($F(1, 31) = 16.46, p < .001$).

Figure 10: Interaction between previous trial feedback type and feedback block for Experiment 3



Explicit monitoring. We first examined the LVF and RVF feedback blocks with a 2 (feedback block: LVF feedback, RVF feedback) X 3 (type of feedback on previous trial: positive, negative, neutral) repeated measures ANOVA on the percent error and latency data. These data are shown in Figures 10 and 11. The results of this experiment look markedly different from Experiments 1 and 2. In the error rate data, there were no significant main effects or interactions. There was no difference between error rate following LVF negative feedback (20.9%) and error rate following RVF negative feedback (21.0%). In the latency data, there was no main effect of feedback block, and no significant interaction between feedback block and type of feedback. There was, however, a significant main effect of previous trial feedback type, $F(2, 62) = 3.18, p < .05$. This was due to slower responses following negative feedback (790 ms) as opposed to positive (766 ms) or neutral (764 ms) feedback. We then analyzed the "Both" blocks with a 2 (visual field of previous trial: left, right) X 2 (type of feedback on previous trial: positive, negative) repeated measure ANOVA for both percent error and latency. There were no significant main effects or interactions found in this data.

Figure 11: Interaction between previous trial feedback type and feedback block for Experiment 3



<u>Implicit monitoring.</u> Data from the control blocks was analyzed with a 2 (correctness of previous trial: correct, incorrect) X 2 (visual field of previous trial: left, right) repeated measures ANOVA for accuracy and latency. The latency data showed no significant slowing after errors (794 ms) compared to after correct trials (781 ms). Nor was there an interaction between previous trial visual field and previous trial correctness. The accuracy data also showed no main effect of previous trial correctness. The interaction between previous trial visual field and previous trial correctness did not reach significance, $F(1, 31) = 2.99, p < .10$. Participants tended to commit fewer errors after an RVF error trial (17.6%) than after an LVF error trial (21.8%), but this result did not reach

significance in a planned comparison, $F(1, 31) = 3.43$, $p < .08$. We ran another analysis with current visual field as the second variable and did not find any significant effects.

Again, all analyses were re-computed with sex as a between-subject variable. There was no main effect of sex, and sex did not interact with any other variable in these data.

DISCUSSION

Experiments 2 and 3 were identical except for the nature of the feedback stimulus, yet they bore out very different results. The verbal feedback seems to have eliminated the interaction found in the first two experiments. This underscores the importance of the type of feedback; some modes of feedback are more effective than others, and each hemisphere may be sensitive to different modes of feedback.

It is possible that the verbal stimulus was more difficult to perceive and therefore was ineffective. This explanation is not satisfying, since participants in this task are making decisions about words that appear very briefly in both visual fields. Another interpretation is that the right hemisphere is specialized for error monitoring in this task, and is unable to use verbal stimuli effectively as feedback. If this is the case, then the right hemisphere advantage in monitoring should reappear when an appropriately designed feedback stimulus is presented.

Experiment 4. **Feedback with spatial signals.**

This experiment was designed to further compliment the hypothesis that different kinds of feedback may be processed more efficiently by one hemisphere than the other. The feedback in this experiment has a spatial component (arrows pointing upward or downward), which is expected to benefit the right hemisphere more than the left. It was expected that the results would be similar to Experiment 1, in which facial emotions were used as feedback. If the effect of feedback in this experiment is as strong as it was in Experiment 1, this would suggest that in general, stimuli which are processed better by the right hemisphere serve as better feedback signals for the lexical decision task.

METHOD

Participants. For this experiment, 32 different UCLA undergraduate students (16 male, 16 female) participated for partial course credit. Only participants who learned English as their first language and were strongly right-handed as determined by a modified Oldfield-Edinburgh handedness inventory were tested. All had normal or corrected-to-normal vision.

Materials and Apparatus. The chinrest setup, response box, computer, and computer software were identical to those used in Experiments 1, 2, and 3. The word lists were identical to those used in Experiments 2 and 3.

Figure 12: Feedback stimuli for Experiment 4

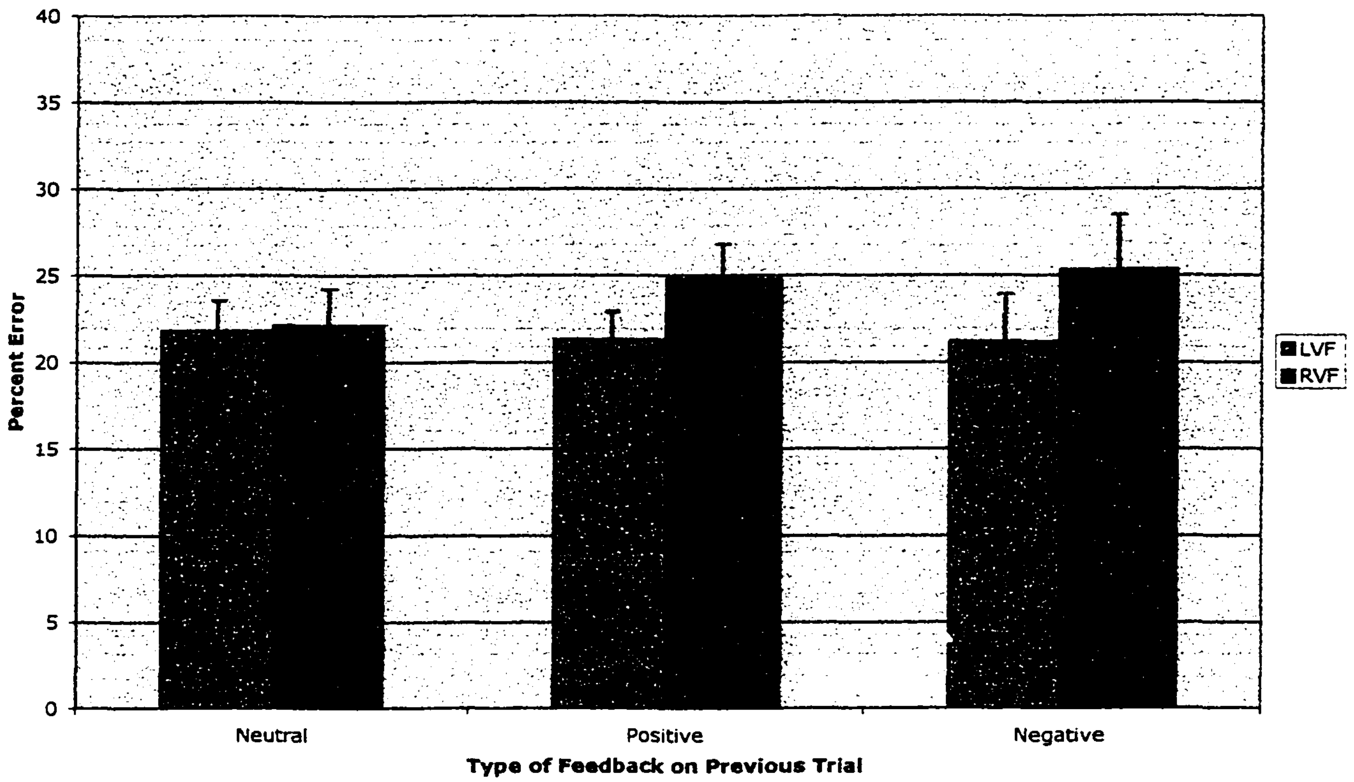
Procedure. The procedure was the same as Experiment 2 except that the feedback stimuli were changed to arrows pointing up to indicate a correct response, or pointing downward to indicate an error. The control stimulus (the neutral feedback) was the line of the arrow without the arrowheads (see Figure 12).

RESULTS

Data points that were greater than 3 standard deviations away from the mean of each cell were discarded.

Lexical decision variables. Once again, to check for the standard lexical decision pattern we conducted a 2 (visual field of target: left, right) X 2 (wordness of target: word, nonword) X 4 (feedback block: control, LVF feedback, RVF feedback, Both) repeated measures ANOVA for both percent error and latency data. We did indeed find the now familiar RVF advantage in both latency and percent error (788 ms for RVF targets, 851 ms for LVF targets, $F(1,31)=34.68, p < .0001$ and 17.5% errors for RVF targets, 27.2% errors for LVF targets, $F(1,31)=68.37, p < .0001$). There was also a significant advantage for word processing (773 ms for words, 867 ms for nonwords, $F(1,31)=79.04$, $p < .0001$ and 18.3% errors for words, 27.4% errors for nonwords, $F(1,31)=13.49$, $p < .001$), and an interaction between wordness and visual field ($F(2,62)=27.8$, $p < .0001$ for latency and $F(2,62)=40.16$, $p < .0001$ for percent error). However, there was no main effect of block, and block did not interact significantly with the other variables.

Figure 13: Interaction between previous trial feedback type and feedback block for Experiment 4

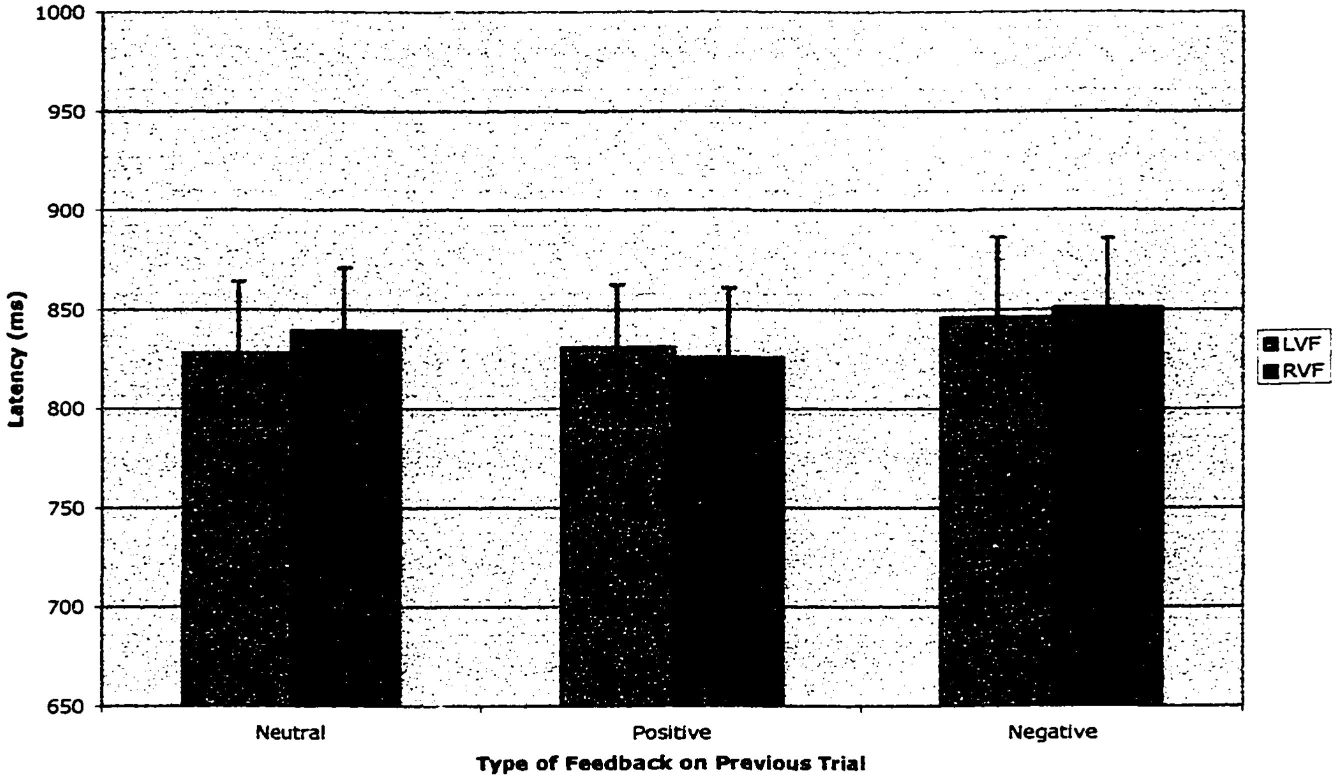


<u>Explicit monitoring</u>. To examine the immediate trial-to-trial effects of feedback we analyzed the LVF and RVF feedback blocks with a 2 (feedback block: LVF feedback, RVF feedback) X 3 (type of feedback on previous trial: positive, negative, neutral) repeated measures ANOVA on the percent error and latency data. The data are shown in

Figures 13 and 14. There were no significant effects in the latency data. In the error data, there was a marginally significant main effect of feedback type ($F(1,31)=2.89, p = .10$), with somewhat fewer errors in the LVF Feedback (21.4%) block compared with the RVF feedback block (24.1%). The interaction between feedback block and type of feedback was not significant, but our hypotheses motivated the planned comparison between trials following negative feedback presented to the LVF or RVF. This comparison was also marginally significant ($F(1,31)=3.2, p = .078$), with more errors following RVF negative feedback (24.8%) compared with LVF negative feedback (21.2%).

Next, we analyzed the "Both" blocks with a 2 (visual field of previous trial: left, right) X 2 (type of feedback on previous trial: positive, negative) repeated measure ANOVA for both percent error and latency. There were no significant effects found in this data.

Figure 14: Interaction between previous trial feedback type and feedback block for Experiment 4



Implicit monitoring. Data from the control blocks was analyzed with a 2 (correctness of previous trial: correct, incorrect) X 2 (visual field of previous trial: left, right) repeated measures ANOVA for accuracy and latency. The difference between trials following errors (820 ms) compared with correct trials (804 ms) was not significant ($F(1,31) = .89, p > .35$). Nor was there a significant interaction between visual field of the previous trial and correctness of the previous trial for latency or percent error. Another analysis with current visual field as the second variable also failed to find any significant evidence of implicit monitoring.

All analyses were re-computed with sex as a between-subject variable. There were no main effects of sex, and sex did not interact with any other variable in these data.

DISCUSSION

We had predicted that the right hemisphere might be more sensitive to a spatial feedback signal. On the contrary, the effect of feedback is diminished compared with the colored squares experiment. This experiment only found very weak evidence of a right hemisphere monitoring advantage. Perhaps the most important quality of the stimulus is its salience, that is, how quickly and easily it can be processed. The colored squares may constitute a more effective error signal because the color is immediately obvious even with a very short presentation. The words and arrows may have required a more difficult discrimination.

Still, the faces produced the strongest effect of all four experiments. This could be due to methodological differences between the experiments. The faces experiment was a between-subjects design, and each subject in the feedback group only performed two conditions: left feedback and right feedback. Performing the feedback blocks in the context of the control and mixed blocks may blur the effect of feedback. We have seen that receiving negative feedback in a mixed LVF/RVF feedback block does not produce the same effect as when the trials are separated out into separate blocks. In this case there is a trial-to-trial context effect. It is conceivable that there is also a block-to-block context effect; for example, responding to feedback could initiate some kind of attentional shift that is long-lasting.

Experiment 5: **Implicit versus explicit monitoring.**

This experiment is designed to further understand the feedback effects found in the first several experiments. Those experiments tested explicit monitoring: error feedback is specifically provided for the participant. In control blocks, participants receive no feedback. Analyses were done to test for implicit monitoring (error processing in the absence of explicit external feedback) in these blocks but none was observed. This is in contrast to the choice reaction time data from Rabbitt (1966a) and to the lexical decision task without feedback from Iacoboni & Zaidel (1996). However, the neutral feedback stimulus appears after every trial, separating the error response from the next response temporally. Processing of this control stimulus may mask the implicit monitoring effects, or there may be too much delay between trials for the error processing to show up as an effect on the subsequent trial. Either way, these experiments do not rule out that there is implicit monitoring going on.

Are the observed feedback effects due to the explicit feedback or are they due to the combined effect of implicit and explicit feedback? In these experiments, participants may have known they were wrong from internal monitoring in addition to being told with our external cues. Experiment 5 is designed to separate more clearly the effects of explicit and implicit monitoring by providing feedback that does not correspond to actual performance. This way, we can compare the effect of feedback when it was meaningful in the previous experiments (it corresponded with actual performance and thus with internal monitoring) to the case when it is meaningless (it conflicts with actual performance and internal monitoring). If the right hemisphere sensitivity to feedback is due simply to a response to the feedback stimulus, then it should respond the same regardless of the veracity of the feedback. If, however, there is a different response to feedback when it is fallacious, this would suggest that implicit monitoring interacts with explicit monitoring.

METHOD

Participants. For this experiment, 32 different UCLA undergraduate students (16 male, 16 female) participated for partial course credit. Only participants who learned English as their first language and were strongly right-handed as determined by a modified Oldfield-Edinburgh handedness inventory were tested. All had normal or corrected-to-normal vision.

Materials and Apparatus. The chinrest setup, response box, computer, and computer software were identical to those used the previous experiments. The word lists were identical to those used in Experiment 2.

Procedure. The procedure was the same as Experiment 2 except that the feedback stimuli were not related to the participants' responses. Feedback was again in the form of blue, yellow, and black squares, but it was presented randomly, with 75% of the trials indicated as correct and 25% as errors. This proportion was chosen as a typical error rate for this task. Participants were told before the experiment that the feedback is informing them about their performance, so they all initially believe the feedback is meaningful. After the experiment, participants were debriefed and given a questionnaire that asked if they noticed that the feedback did not actually correspond to their performance.

RESULTS

Data points that were greater than 3 standard deviations away from the mean of each cell were discarded.

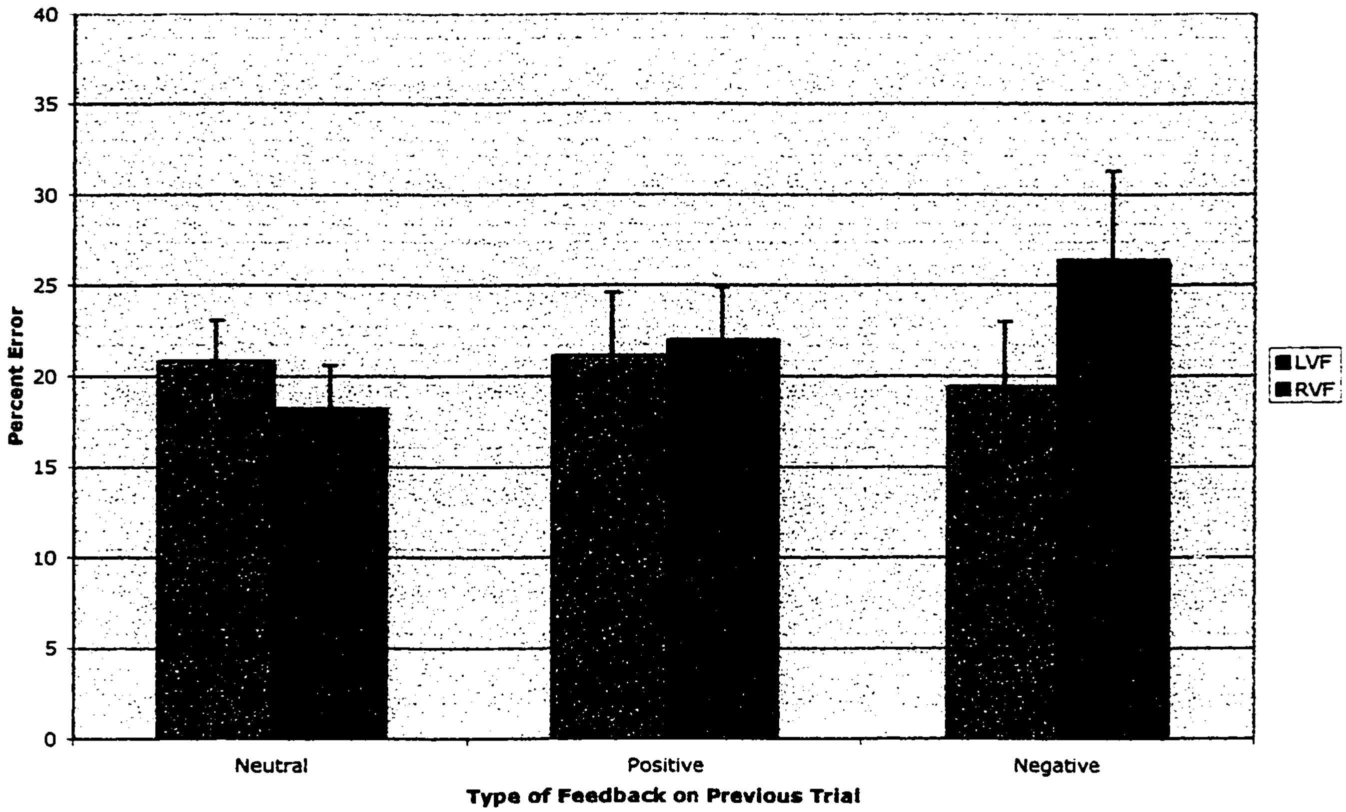
Lexical decision variables. The standard lexical decision pattern was examined with a 2 (visual field of target: left, right) X 2 (wordness of target: word, nonword) X 4 (feedback block: control, LVF feedback, RVF feedback, Both) repeated measures ANOVA for both percent error and latency data. The RVF advantage was significant (747 ms LVF, 785 ms RVF, $F(1,31)=8.34, p < .01$ and 16.2% RVF, 26.5% LVF, $F(1,31)=41.8, p < .001$). The wordness advantage was significant in latency (724 ms for words, 808 ms for nonwords, $F(1,31)=58.24, p < .0001$) and approached significance in accuracy (18.6% errors for words, 24.2% errors for nonwords, $F(1,31)=4.06, p = .056$). The wordness by visual field interaction was present in the latency ($F(3,93)=17.47, p < .001$) and percent error ($F(3,93)=16.21, p < .001$) data. There was no main effect of feedback block, and this variable did not interact significantly with the others.

Explicit monitoring. To examine the immediate trial-to-trial effects of feedback we analyzed the LVF and RVF feedback blocks with a 2 (feedback block: LVF feedback, RVF feedback) X 3 (type of feedback on previous trial: positive, negative, neutral) repeated measures ANOVA on the percent error and latency data. This analysis examined the effect that feedback had on the subsequent trial regardless of its veracity. The latency data showed a significant effect of previous trial feedback type ($F(2,62)=15.38, p < .0001$). Subjects were slower on trials following negative feedback (820 ms) compared with positive (773 ms) or neutral feedback (755 ms), even though this feedback was most often false. No significant effects emerged from the analysis of error data. However, when sex of the subject was added to the analysis as a between-subjects variable, there was a significant three way interaction between feedback block, type of feedback, and sex ($F(2,60=4.31, p < .02$) in the error data. This sex interaction did not show up in the latency data.

The interaction with sex motivated an analysis of male and female subjects separately. For female subjects, the interaction between feedback block and type of feedback in the percent error data yielded $F(2,30)=2.69$, with $p = .084$ (see Figure 15). The key planned comparison between trials following LVF negative feedback compared with RVF negative feedback was significant, $F(2,30)=5.613, p = .025$. Trials following RVF negative feedback (26.4%) had a higher error rate than trials following LVF negative feedback (19.4%). This is the pattern we have observed in the other experiments, where negative feedback leads to more errors when presented in the RVF. Males, on the other hand, showed a different pattern (see Figure 16). For males, the interaction between previous trial feedback type and block yielded $F(2,30)=2.36, p = .11$. The planned comparison between trials following LVF negative feedback and RVF negative feedback showed a significant result ($F(2,30=5.02, p = .03$), but in the opposite direction from the females. Trials following RVF negative feedback had fewer errors

(21.7%) than trials following LVF negative feedback (29.8%). Better performance following negative feedback presented to the left hemisphere was not seen in any of the other experiments, suggesting that the males were sensitive to the falsity of the feedback.

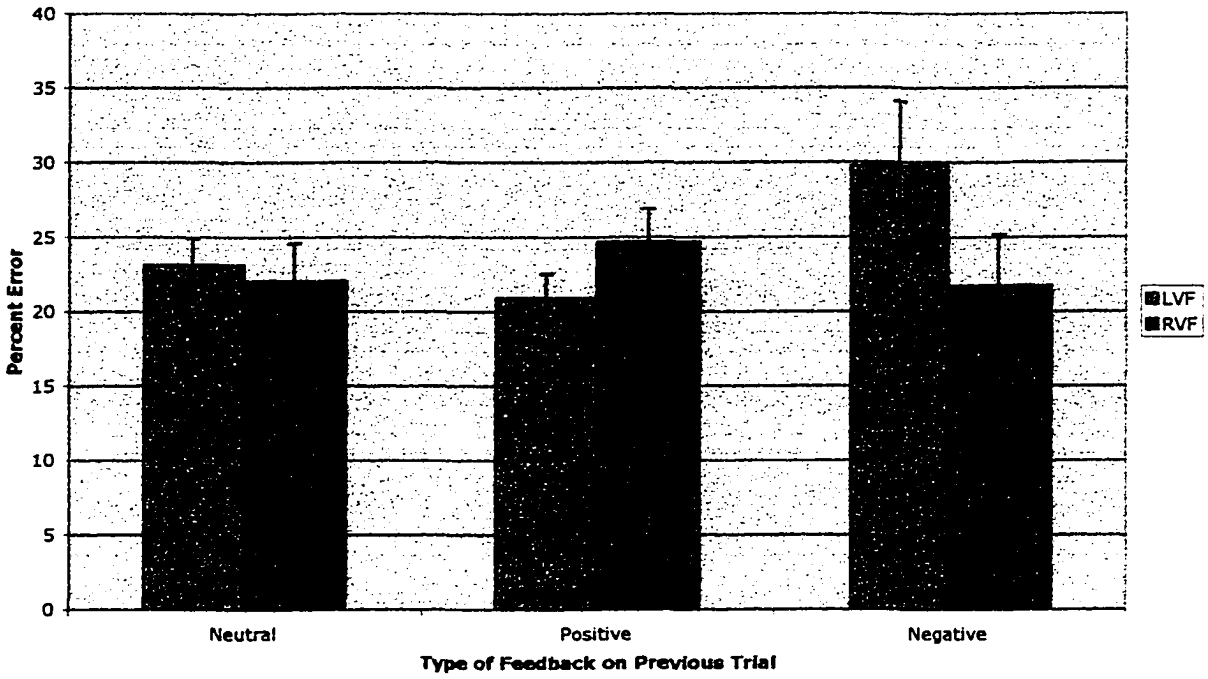
Figure 15: Data for Females in Experiment 5



The "Both" blocks were analyzed with a 2 (visual field of previous trial: left, right) X 2 (type of feedback on previous trial: positive, negative) X 2 (sex: male, female) repeated measure ANOVA for both percent error and latency. There were no significant effects in this analysis.

Implicit monitoring. The sex difference found in the explicit monitoring data motivated the inclusion of sex as a variable in the implicit monitoring analysis. Data from the control blocks was analyzed with a 2 (correctness of previous trial: correct, incorrect) X 2 (visual field of previous trial: left, right) X 2 (sex: male, female) ANOVA for accuracy and latency. The latency data showed no significant effects. In the error data, the three way interaction between correctness of the previous trial, visual field of the previous trial, and sex approached significance, $F(1,28)=3.83, p = .06$. Once again, data for males and females were analyzed separately to examine the pattern for each sex.

Figure 16: Data for Males from Experiment 5



Males showed a significant interaction between previous trial correctness and visual field of the previous trial ($F(1,15)=11.2, p < .01$). The planned comparison between trials following LVF errors and RVF errors was significant ($F(1,15)=10.93, p < .01$). Performance was better following LVF errors (17.6% errors) compared with RVF errors (27.9% errors). For females, none of these effects were significant. The implicit monitoring analyses were also conducted with the current visual field as a variable instead of the previous visual field and did not find any significant main effects or interactions.

Since the feedback is given randomly, there are trials in which the feedback is accurate and trials in which it is false. Unfortunately, there are not enough instances where errors co-occurred with negative feedback to perform an analysis comparing true and false feedback.

DISCUSSION

The most interesting result of this experiment concerns a sex difference in the interaction between implicit and explicit monitoring. The females reacted to the false feedback in the same way that subjects reacted in Experiment 2, when the feedback was real. Males, however, had a different reaction, responding better when the negative feedback was presented to the left hemisphere. This could reflect a shift in explicit feedback processing based on increased implicit monitoring. When the feedback indicates an error (explicit monitoring), but the subject knows that a correct response was made (implicit monitoring), the reaction to the feedback signals can be adjusted. Males did in fact show increased evidence of implicit monitoring in control blocks, a result that was elusive in the other experiments. Males performed better following LVF error trials, a result consistent with the one found by Iacoboni, Rayman and Zaidel (1997). In other words, if males realized that the feedback was false, they may have shifted to relying on their own sense of their correctness instead of trusting the feedback signals. In this case their response to a negative feedback stimulus would no longer relate to its value as an indicator of performance. Instead, their reaction to the explicit negative feedback may reflect a noticed discrepancy between the results of implicit monitoring and the explicit feedback stimulus.

Females did not show evidence of this adjustment. This could reflect a difference in implicit monitoring between males and females, or a difference in how implicit and explicit monitoring conflicts are resolved. If the females did not notice that the feedback stimuli were false they could not change their interpretation of them. However, even if they did recognize the falsity of the feedback they may have still trusted the feedback signals over their implicit monitoring. A post-experimental questionnaire asked if the subjects had noticed the falsity of the feedback. All but three subjects (two male and one female) reported that they noticed that the feedback was false. However the wording of the question was rather suggestive ("Did you notice that the feedback was not always an accurate indication of your performance?").

A sex difference in implicit monitoring was also found by Zaidel et al. (1998). In this meta-analysis of lexical decision experiments, males showed an interaction between previous trial correctness and visual field of the previous trial, while females did not. These data confirm that there is a sex difference in implicit monitoring that interacts with hemispheric specialization for monitoring. The interaction with hemispheric specialization may relate to a sex difference in amygdala function. Cahill et al. (2001) found that amygdala activation during encoding of negative emotional films correlated with subsequent recall of those films. For females, activity in the right amygdala correlated with recall, while for males the correlation was in the left amygdala. Processing negative feedback may involve neural circuitry for emotional evaluation, a hypothesis supported by neuroimaging evidence described later in this dissertation.

It is interesting to note that implicit monitoring effects depend on the visual field of the previous trial, and not on the visual field of the current trial. This means that the when an error is detected, a reaction to that error is initiated by the hemisphere which committed the mistake, but this reaction affects processing in both hemispheres similarly.

Experiment 6. **Feedback to the uninvolved hemisphere.**

This experiment is designed to address some of the issues relating to the dynamics of error processing. It is conceivable that the two hemispheres function more optimally when they divide labor between them. If one hemisphere is engaged in the cognitive processing related to a task, that might free the other hemisphere to participate in monitoring and control (Zaidel, 1987). Alternatively, feedback may only be effective if the hemisphere that is doing the task gets it directly. Transferring the feedback across the corpus callosum should degrade the stimulus. Therefore if the effects of feedback are attenuated when target stimulus and feedback stimulus are sent to opposite hemispheres, this would be evidence for the "each hemisphere needs its own feedback" hypothesis, If, however, the effects of feedback are increased, this would be taken as evidence of the "labor sharing" hypothesis.

In all of the previous experiments, feedback was presented in the same visual field as the target. In contrast, this experiment will present feedback in the visual field opposite to the one where the target was presented. In the lexical decision task, we expect the hemisphere which initially receives the stimulus to perform the lexical processing. In this experiment the hemisphere that is doing the lexical processing will only be able to receive feedback that has been shuttled across the corpus callosum from the other hemisphere.

METHOD

Participants. For this experiment, 32 different UCLA undergraduate students (16 male, 16 female) participated for partial course credit. Only participants who learned English as their first language and were strongly right-handed as determined by a modified Oldfield-Edinburgh handedness inventory were tested. All had normal or corrected-to-normal vision.

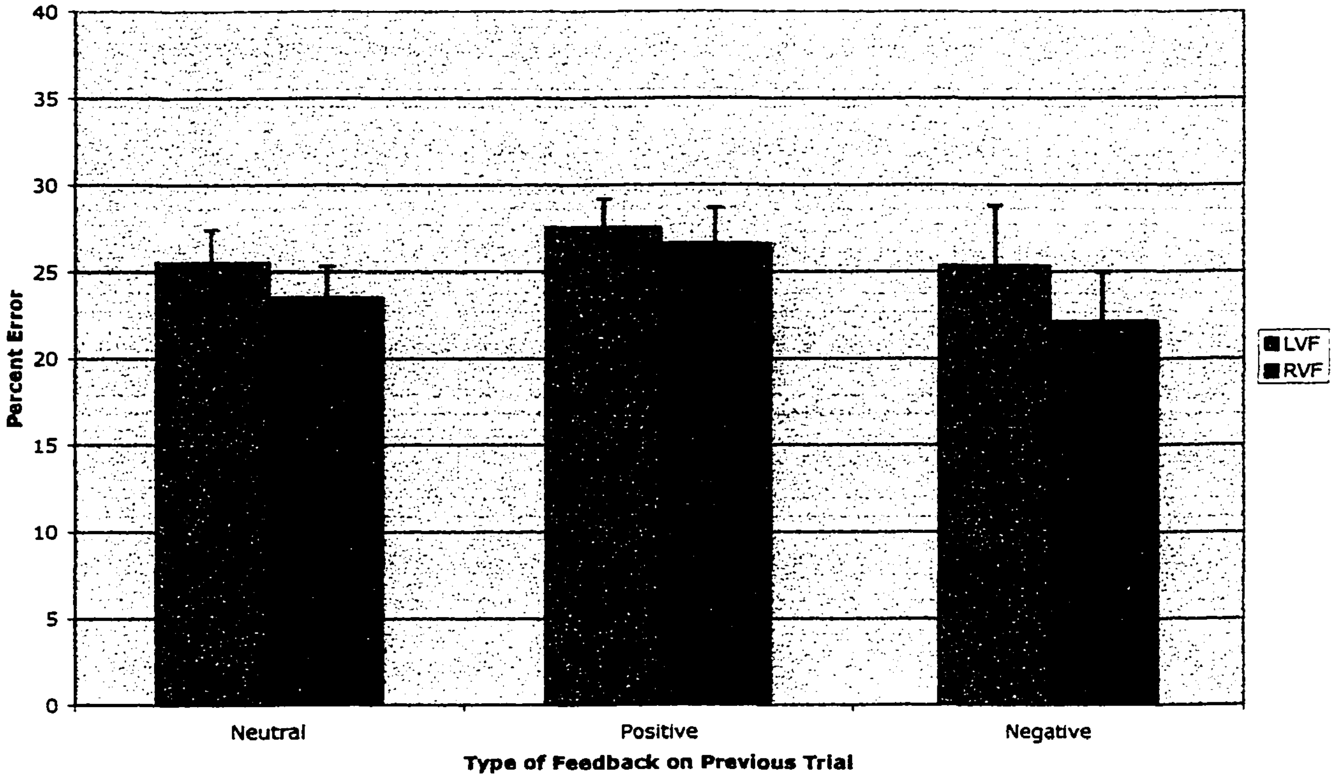
Procedure. The procedure was the same as Experiment 2 except that the when targets are presented in the LVF, feedback is presented in the RVF. When the target is presented in the LVF, feedback is presented in the LVF.

RESULTS

Data points that were greater than 3 standard deviations away from the mean of each cell were discarded.

Lexical decision variables. We conducted a 2 (visual field of target: left, right) X 2 (wordness of target: word, nonword) X 4 (feedback block: control, LVF feedback, RVF feedback, Both) repeated measures ANOVA for both percent error and latency data. In the latency data, all three lexical decision effects were significant: the right visual field advantage (718 ms RVF, 145 ms LVF, $F(1,31)=7.68, p < .01$), the wordness advantage (699 ms words, 763 ms nonwords, $F(1,31)=14.08, p < .001$), and the visual field X wordness interaction ($F(1,31)=21.30, p < .0001$). There was no main effect of feedback block, and this variable did not interact significantly with the others. In the error data, the right visual field advantage was significant (19.9% errors RVF, 29.5% errors LVF, $F(1,31)=38.07, p < .0001$), as was the visual field X wordness interaction ($F(1,31)=52.25, p < .0001$). The wordness advantage was not quite significant (22.4% errors for words, 27% errors for nonwords, $F(1,31)=3.56, p =.068$). Feedback block did not show a significant main effect or any interactions.

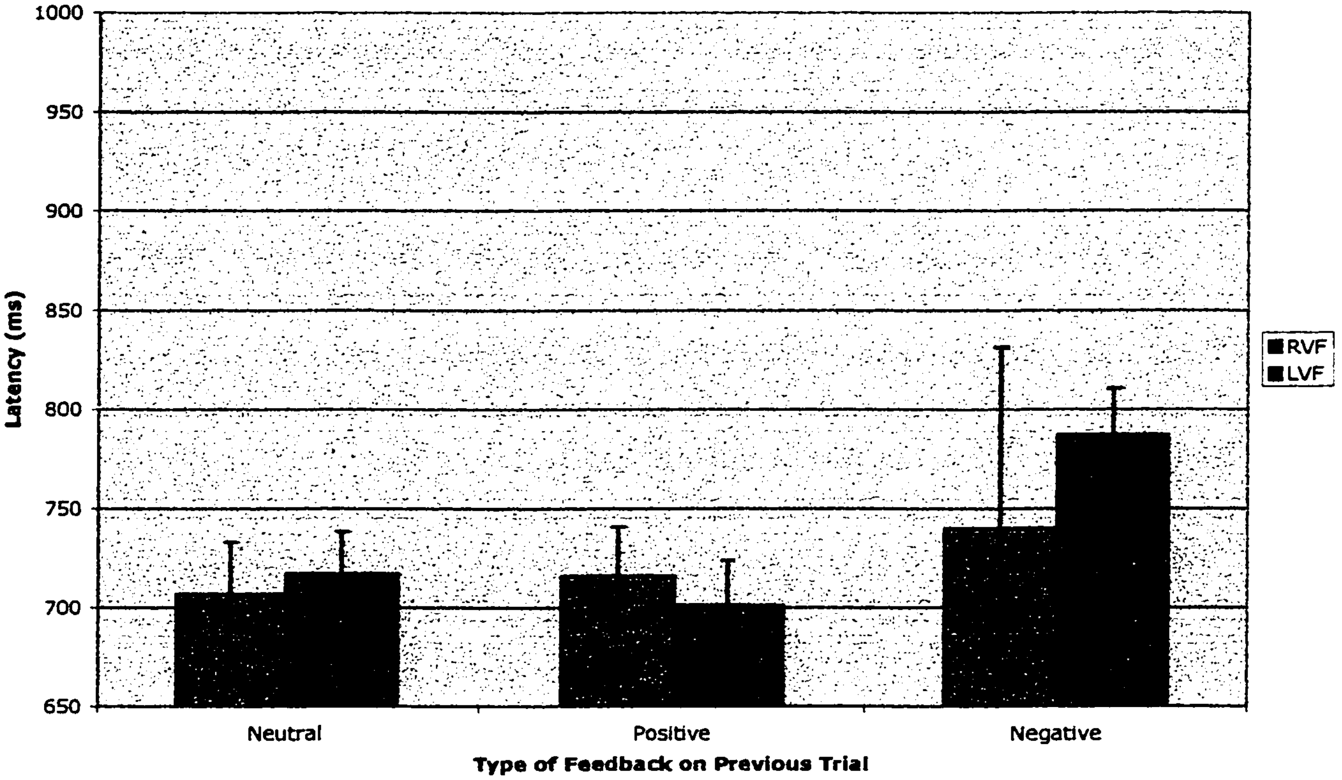
Figure 17: Interaction between previous trial feedback type and feedback block



Explicit monitoring. We examined the LVF and RVF feedback blocks with a 2 (feedback block: LVF feedback, RVF feedback) X 3 (type of feedback on previous trial: positive, negative, neutral) repeated measures ANOVA on the percent error and latency data. These analyses yielded no significant effects (see Figures 17 and 18).

Next, we analyzed the "Both" blocks with a 2 (visual field of previous trial: left, right) X 2 (type of feedback on previous trial: positive, negative) repeated measure ANOVA for both percent error and latency. There were no significant effects in the latency data. The error data showed a main effect of previous trial visual field; subjects made fewer errors following LVF trials (23.5%) than following RVF trials (28.9%).

Figure 18: Interaction of previous trial feedback type and feedback block for Experiment 6



Implicit monitoring. Data from the control blocks was analyzed with a 2 (correctness of previous trial: correct, incorrect) X 2 (visual field of previous trial: left, right) repeated measures ANOVA for accuracy and latency. There were no significant effects found, thus there is no evidence here of implicit monitoring. We also conducted the analysis with current visual field as the second variable and again found no evidence of implicit monitoring.

All analyses were re-computed with sex as a between-subject variable. There were no main effects of sex, and sex did not interact with any other variable in these data.

DISCUSSION

In previous experiments, feedback had always been presented in the same visual field as the target letter string. Here, we presented feedback in the opposite visual field and did not find any significant effects of the feedback. Thus, subjects did not show evidence of explicit monitoring when the task stimulus and the performance feedback were presented to separate hemispheres.

This could indicate that for feedback information to be utilized, it must be processed by the hemisphere that was engaged by the task. In this model, self-monitoring is module-specific; that is, each cognitive unit can only monitor its own functioning. It would not be a surprise to find such independence in hemispheric functioning; in fact, the bilateral presentations are designed specifically to increase independent hemispheric processing (Iacoboni & Zaidel, 1996).

However, there is an alternative explanation. The target word may have served as an attentional cue, drawing the subject's attention to one visual field. Then, when the feedback appeared in the opposite visual field, it was relatively unattended. If attention is required for explicit self-monitoring, then the feedback could be expected to have a diminished effect.

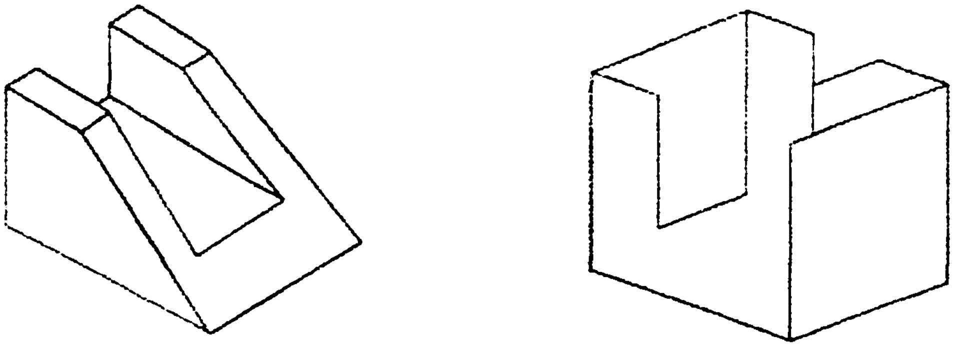
There was evidence of explicit monitoring in the "Both" blocks. In those blocks, subjects made fewer errors following LVF trials. In these blocks, LVF targets were always followed by RVF feedback. This means that the only evidence of monitoring in this experiment was when the right hemisphere processed the stimulus and the left hemisphere received the feedback stimulus, within the context of a mixed block. The mixed blocks may lead to a situation in which attention is divided more evenly across the visual fields, compared with blocks in which feedback repeatedly appears on one side. Since attention was distributed rather than focused in these blocks, there may have been more cross-hemispheric cooperation. This would explain why there was an effect of feedback in the mixed blocks but not in the LVF and RVF feedback blocks.. It is interesting that in these blocks subjects improved following RVF feedback. It may be that the right hemisphere monitoring advantage in lexical decision is due to the way in which the right hemisphere processes the stimulus, rather than the way the right hemisphere processes the feedback. In other words, right hemisphere lexical processing may be more adjustable in response to feedback, regardless of which hemisphere processes the feedback stimulus.

Experiment 7. **Feedback in an object classification task.**

Even though we regard the lexical decision task as a "direct access" task and both hemispheres are capable of making lexical decisions (Zaidel et al., 1990), the decision is performed more quickly and accurately by the left hemisphere. Experiments 1-6 have corroborated this by finding a right visual field advantage in the task overall. It is possible that the right hemisphere response to feedback reflects its inferior competence in the task. If error monitoring responsibilities are shifted dynamically in response to the demands of the current task, the inferior hemisphere may be delegated the monitoring role to allow the dominant hemisphere to focus on the original task. To test this hypothesis, lateralized feedback will be provided in a task that is expected to show a right hemisphere advantage. The task chosen is an object perception/classification task adapted from experiments performed by Schacter and colleagues (Schacter & Cooper, 1993; Schacter, Cooper, & Delaney, 1990). Participants are shown drawings of three-dimensional objects, some of which have structural violations that make it impossible for them to exist in three-dimensional space. Half of these drawings could be real objects, but half of them are "impossible" objects (see Figure 19). A previous experiment has indicated a right hemisphere superiority for this task (Smith, Tays, Dixon, & Bulman-Fleming, in press). This experiment will also allow testing of the generality of the previous results. Does the right hemisphere sensitivity to feedback extend to other tasks? Alternatively, does the nondominant left hemisphere assume the monitoring functions for this task?

METHOD

Participants. For this experiment, 32 different UCLA undergraduate students (16 male, 16 female) participated for partial course credit. Only participants who are strongly right-handed as determined by a modified Oldfield-Edinburgh handedness inventory were tested. All had normal or corrected-to-normal vision.



possible object

impossible object

Figure 19: Stimuli from Experiment 7, the object decision task

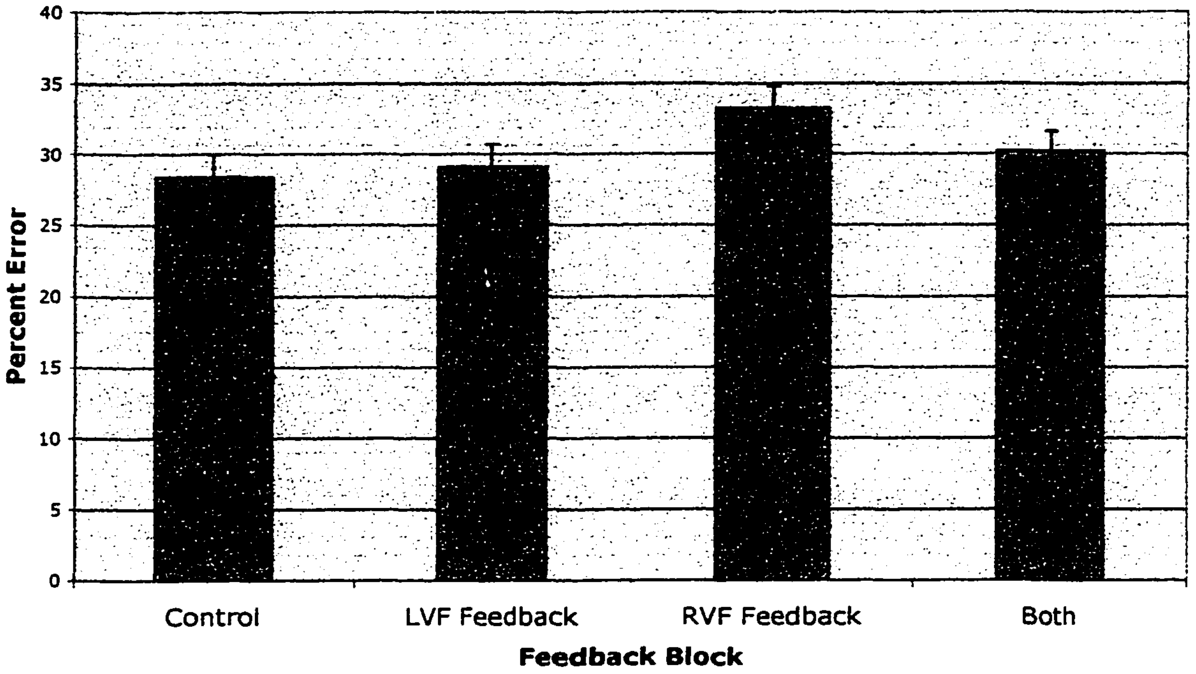
Materials & Apparatus. Stimuli consisted of 12 possible objects and 12 impossible objects from the set used by Schacter, Cooper, and Delaney (1990). Sample stimuli are presented in Figure 19. Pictures were presented in a square subtending 6.5° by 6.5° of visual angle, with the inner edge 1.25° away from fixation. Each block consisted of 72 trials, so each picture was seen three times per block.

Procedure. The design of this experiment is similar to Experiment 2 except that the decision to be made is whether the object is possible or impossible. One object appears on the screen at a time, either in the LVF or in the RVF, for 150 ms. After a response is made, feedback in the form of colored squares presented for 150 ms. Just as in the previous experiments, for half of the participants, a blue square indicated a correct response, and a yellow square indicated an error. For the other half of the participants, the colors were reversed. A black square always served as neutral feedback and did not provide any information about accuracy. The feedback stimulus appeared only in the visual field where the target had been. After a 16-trial practice block there were four blocks of trials. In one block, the control block, a black square was presented after each trial. In the LVF Feedback block, accuracy feedback appeared after all LVF trials, and a black square appeared after all RVF trials. In the RVF Feedback block, feedback was presented only after RVF trials, and LVF trials were followed by the neutral stimulus. In a fourth block, feedback appeared after every trial.

RESULTS

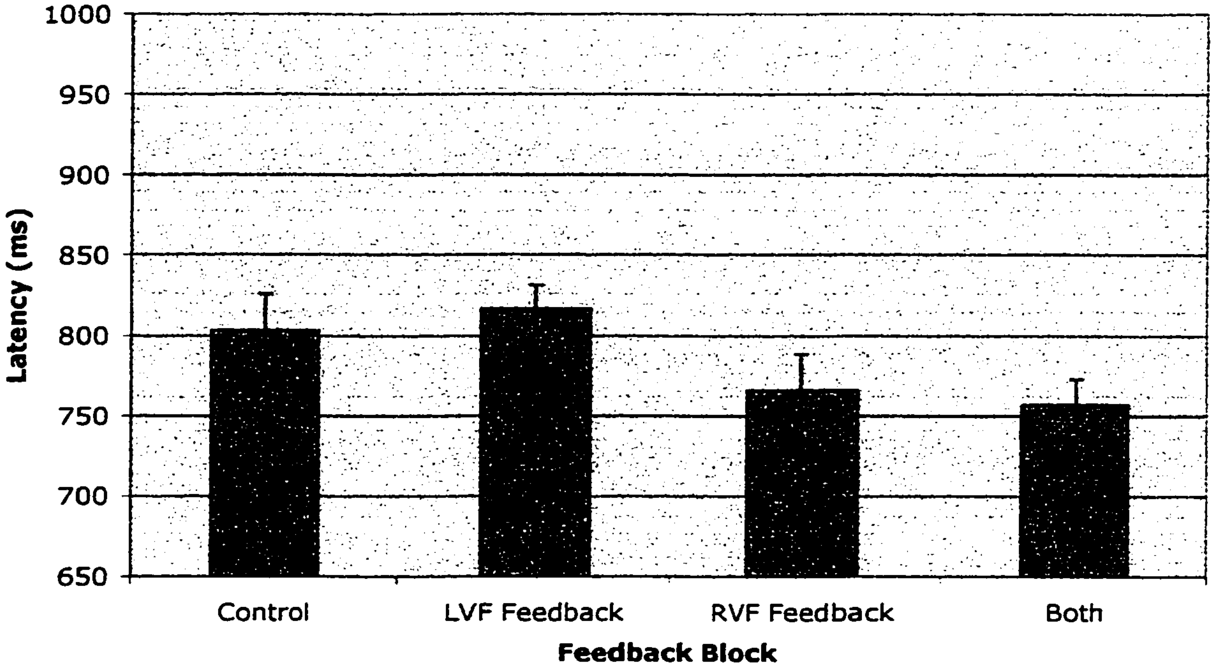
Visual field and possibility effects. The latency and error data were submitted to a 2 (visual field: left, right) X 2 (possibility: impossible, possible) X 4 (block: Control, LVF feedback, RVF feedback, Both) repeated measures ANOVA. The data showed a LVF advantage for object decisions, with fewer errors in the LVF (26.2%) compared with the RVF (34.4%), ($F(1,31)=55.12, p < .0001$), and faster responses in the LVF (776 ms) compared with the RVF (795 ms) ($F(1,31)=14.67, p <.001$). Subjects also performed significantly better with possible objects than with impossible objects. With possible objects, subjects made 25.7% errors and with impossible objects they made 34.8% errors ($F(1,31)=15.74, p < .001$). Responses were faster for possible objects (776 ms) than for impossible objects (795 ms) ($F(1,31)=7.23\ p < .02$).

Figure 20: Effect of Feedback Block for Experiment 7



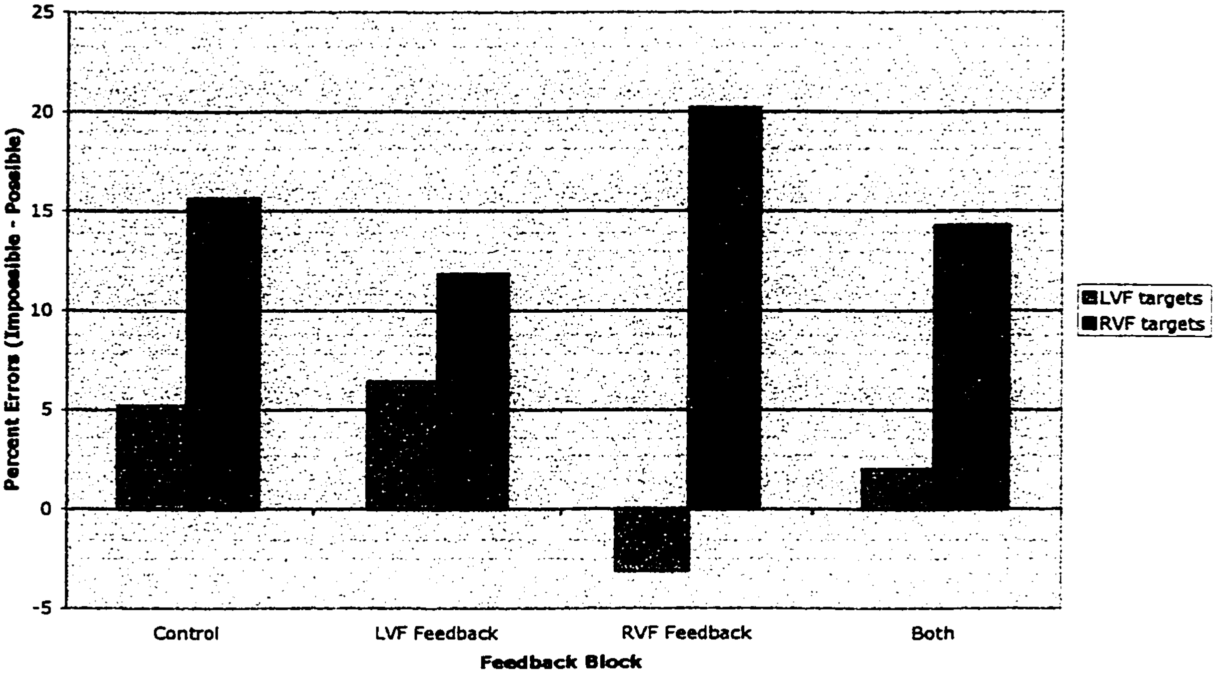
The error data showed a significant main effect of feedback block ($F(3,93)=3.17$, $p < .03$), shown in Figure 20. Planned comparisons revealed that only the RVF feedback blocks were significantly different from control blocks ($F(1,31)=8.11$, $p < .01$). In Control blocks, subjects made 28.4% errors, while in RVF feedback blocks, error rate increased to 33.2%. The latency data did not show a significant main effect of block, but RVF Feedback blocks and Both blocks were about 40 ms faster than control blocks (see Figure 21). In the error data, there was a significant interaction between visual field and possibility ($F(1,31)=12.69$, $p < .01$), reflecting a greater possibility effect in the RVF. The data also showed a three way interaction between block, visual field, and possibility ($F(3,93)=4.1$, $p < .01$). This interaction is shown in Figure 22 as the difference in error rate between impossible and possible object trials, plotted for each block by visual field. This figure shows that the possibility effect was modulated in the RVF feedback blocks.

Figure 21: Effect of Feedback block in Experiment 7



The shift in the possibility effect suggests that subjects may have shifted their response bias in these blocks. In order to examine this effect further, we decided to conduct a signal-detection analysis of the data, treating possible objects as the signal. We computed *d'* and the natural logarithm of β and submitted these values to a 2 (visual field of target: left, right) X 4 (block: Control, LVF Feedback, RVF Feedback, Both) repeated measures ANOVA. For *d'* values there was a significant main effect of block (F(3,93)=3.21, p = .026), a significant main effect of visual field (F(1,31)=52.04, $p <$ .001), and a significant interaction between the two variables (F(2,93)=3.75, p = .014). This interaction in shown in Figure 23. This pattern parallels the error rate data. For log β values there was a significant main effect of visual field (F(1,31)=9.68, $p < .01$) with a greater negative bias in the RVF (-.35) than in the LVF (-.08), but no significant effect of feedback block and no interaction between the two variables (see Figure 24). Thus, we did not find evidence of a response bias shift in response to feedback.

Figure 22: Possibility effect in each visual field by block



The next analysis looked at practice effects across the four blocks of trials with a 4 (session: first, second, third, fourth) X 2 (visual field: left, right) X 2 (possibility: possible, impossible). There was a main effect of session in the error data indicating a strong practice effect ($F(3,93)=30.86, p < .0001$). Error rate went from 36.5% in the first session to 24.8% in the final session. This effect was also present in the latency data, where reaction times went from 900 ms in the first session to 722 ms in the fourth ($F(3,93)=17.34, p < .0001$). In latency, session interacted with visual field, *F*(3,93)=3.24, $p < .05$). These data show a LVF advantage in all sessions except the second. In the percent error data, there was a threeway interaction between session, visual field, and possibility (*F*(3,93)=5.51, $p < .01$). In the first session, the possibility effect was greater in the LVF than in the RVF, but over time the possibility effect became substantially larger in the RVF compared with the LVF.

Figure 23: Block by Visual Field Interaction for d'

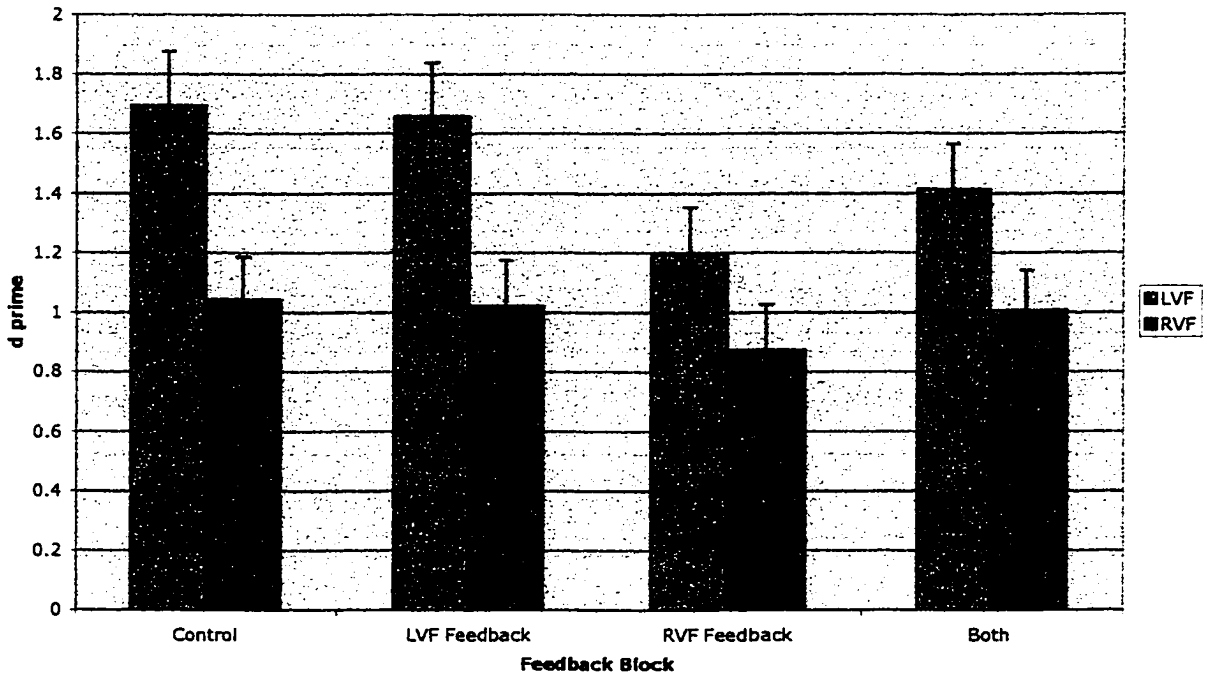
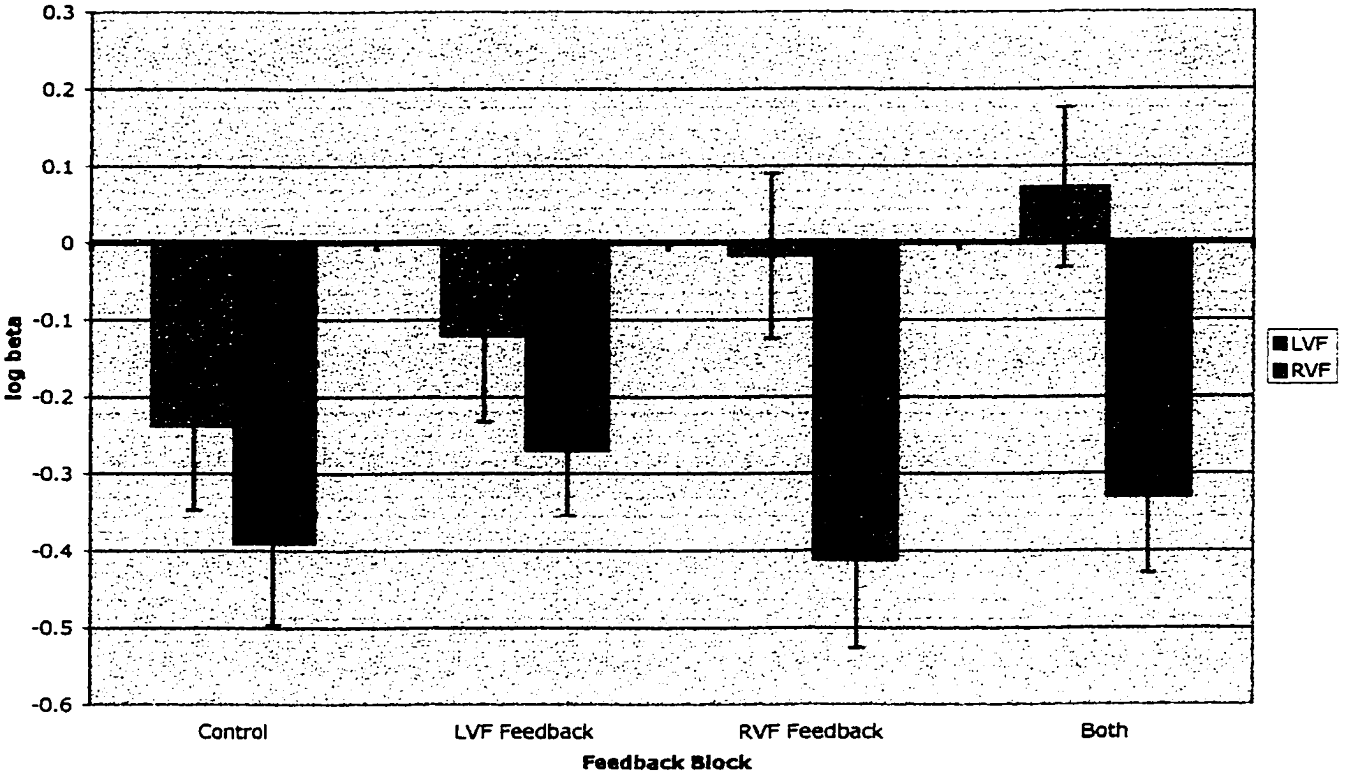
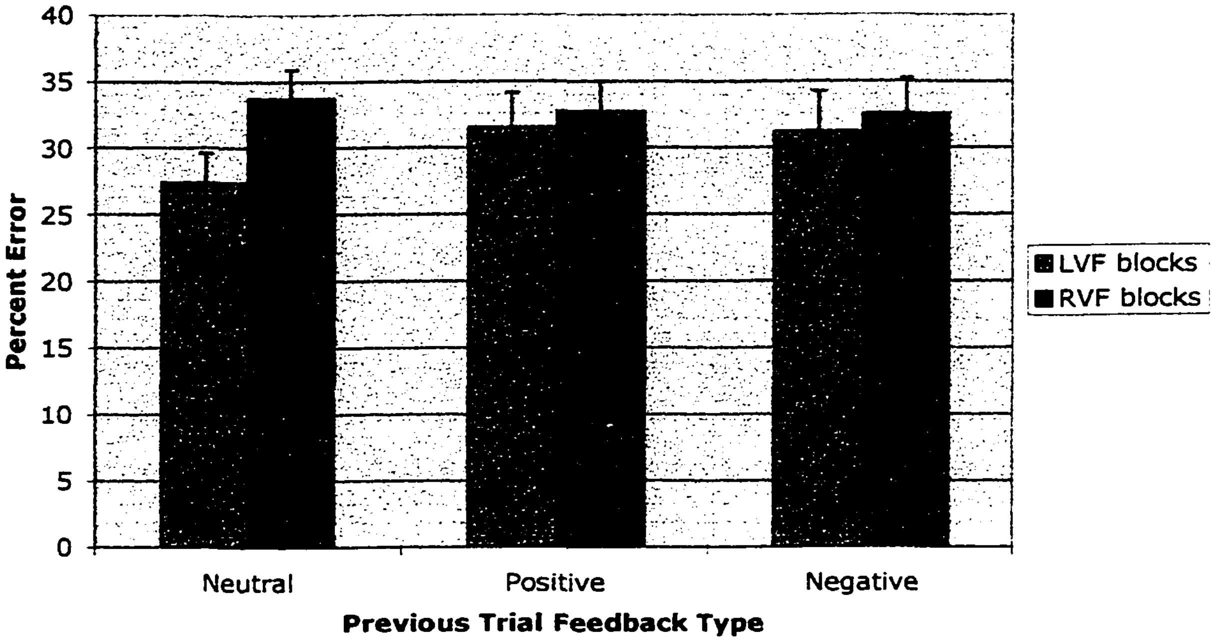


Figure 24: Interaction between Block and Visual Field for Response Bias



Explicit monitoring. We examined the LVF and RVF feedback blocks with a 2 (feedback block: LVF feedback, RVF feedback) X 3 (type of feedback on previous trial: positive, negative, neutral) repeated measures ANOVA on the percent error and latency data. The interaction between previous trial feedback type and feedback block in the error data was marginally significant, F(2,62)=3.04, $p = .055$ (see Figure 25). The only condition that appears different from the others are the trials following LVF neutral feedback. Planned comparisons showed that trials following LVF neutral feedback had fewer errors than trials following negative feedback (F(2,62)=5.18, $p < .05$) and trials following positive feedback (F(2,62)=5.98, $p < .05$). The latency data did not show any significant effects, although there was an indication of slower responses in the LVF feedback blocks (825 ms) compared with the RVF feedback blocks (774 ms), $F(1,31)=2.1, p=.16$.

Figure 25: Interaction between previous trial feedback type and feedback block for Experiment 7



Next, we analyzed the Both blocks with a 2 (visual field of previous trial: left, right) X 2 (type of feedback on previous trial: positive, negative) repeated measure ANOVA for both percent error and latency. The latency data did not show any significant effects. In the error data, however, there was a significant main effect of previous trial visual field, with performance better following RVF trials (28.3% errors) compared with LVF trials (32.3% errors), $F(1,31)=9.56, p<.01$).

Implicit monitoring. Data from the control blocks was analyzed with a 2 (correctness of previous trial: correct, incorrect) X 2 (visual field of previous trial: left, right) repeated measures ANOVA for accuracy and latency. There was no evidence of implicit monitoring in these data. The same analysis was repeated substituting the visual field of the current trial as the second variable and found no significant main effects or interactions related to the correctness of the previous trial.

All analyses were re-computed with sex as a between-subject variable. There were no main effects of sex, and sex did not interact with any other variable in these data.

DISCUSSION

This task showed a LVF advantage as expected, indicating right hemisphere specialization for this task. The interaction between possibility of the objects and visual field of presentation revealed that the left hemisphere had particular difficulty with the impossible objects.

Comparison of the four blocks suggests that the left hemisphere was more sensitive to performance feedback. The RVF feedback blocks were less accurate than the others. Performance also seemed somewhat faster in the RVF feedback blocks and the Both blocks. Although this difference was not statistically significant, it may reflect a speed-accuracy tradeoff initiated by the left hemisphere in response to feedback. Subjects may have adjusted their strategy to respond more quickly since they were receiving mostly positive feedback. The possibility effect was also altered in the RVF feedback blocks, confirming that a shift in processing strategy occurred when the left hemisphere was receiving feedback. However, the data did not support the idea that this strategy shift was simply an adjustment of response criterion, since there was no significant effect of feedback block on β values.

Curiously, while the RVF feedback blocks were less accurate overall than control blocks, performance did not seem to be modulated by the type of feedback on the previous trial in these blocks. Only in LVF feedback blocks was performance influenced by the previous trial, and in this case it was sensitive only to the presence of feedback rather than the type of feedback as we have seen before. Subjects were more accurate on trials following neutral feedback compared with trials following positive and negative feedback. Remember that in LVF feedback blocks, if the previous trial received neutral feedback then it must have been a RVF target, since in these blocks RVF targets are followed by neutral feedback stimuli. However, this effect is not simply an effect of previous trial visual field, since in the control blocks performance does not depend on the visual field of the previous trial. This effect could be interpreted as a local effect LVF feedback; any feedback stimulus presented in the LVF decreases accuracy on the next trial relative to a control stimulus. In the RVF feedback blocks, all trials were less accurate regardless of the type of feedback on the previous trial. To summarize, LVF feedback caused a general, local feedback effect that was independent of the valence of the feedback stimulus. RVF feedback, on the other hand, produced a global effect that changed task strategy and affected all trials within the block.

In the lexical decision experiments, where we found a right hemisphere sensitivity to feedback, there tended to be only local effects of feedback. It may be that the left hemisphere control mechanisms work by adjusting long term processes that affect the task (such as strategy shifts, speed-accuracy tradeoffs, etc.) whereas the right hemisphere mechanisms make immediate, short-term adjustments (for example, increasing focus on the subsequent trial). It important to note, however, that the left hemisphere sensitivity to feedback involved a decrease in performance. A decrease in performance following feedback presented to the left hemisphere was also found in the lexical decision experiments, where there was a local effect of negative feedback presented to the left hemisphere. The left hemisphere may be reacting to the feedback by initiating strategy shifts that lead to non-optimal performance.

This task showed a rather strong practice effect. Since the order of feedback blocks was counterbalanced, it is not clear how the presence of feedback might relate to learning in this task. It is conceivable that feedback affects the rate of learning of object decisions, and that this effect could interact with hemifield of presentation. This would be an interesting subject for further experimentation.

The finding of a left hemisphere sensitivity to feedback in the object decision task suggests that hemispheric feedback processing depends on the nature of the task being monitored. In these experiments, the non-specialized hemisphere has been more responsive to performance feedback. One explanation is the "limited resources" theory. It is possible that the specialized hemisphere is "busy" processing the stimulus, leaving the non-specialized hemisphere to perform monitoring functions. This explanation assumes that that the specialized hemisphere is more engaged by the task at hand. In an extreme version of this assumption, all stimuli are processed by the specialized hemisphere regardless of the visual field of presentation. This is known as the "callosal relay" model since stimuli presented to the unspecialized hemisphere must be relayed across the corpus callosum for processing (Zaidel et al., 1990). While previous data suggests that lexical decisions are made independently by each hemisphere, neuroimaging results in this dissertation will support left-hemisphere processing of LVF stimuli. If stimuli are shuttled across to the specialized hemisphere, then the limited resources theory would be supported. In this case, the hemisphere not engaged by the task has more resources available for feedback processing.

Another explanation does not require callosal relay of the stimulus. This theory relies on evidence that the processing of the task proceeds by a different mechanism in each hemisphere, and that one mechanism is more amenable to feedback-induced adjustments. For example, the specialized hemisphere's processing may be more automatized and less flexible than processing in the non-specialized hemisphere. This would allow the non-specialized hemisphere to make adjustments in response to feedback. There is evidence from both of these tasks that processing is not the same in the two hemispheres. In lexical decision, there is a wordness advantage for RVF stimuli but not for LVF stimuli. In the object decision task, there is a possibility effect in the RVF but not in the LVF.

Experiment 8: **Error detection in the split brain**

A crucial methodology for comparing the function of the two hemispheres involves testing commissurotomy patients, a case in which the hemispheres can be expected to exhibit maximal independence. This experiment tests two split-brain patients' ability to detect and correct their errors in a modified version of the flankers task. As opposed to the previous experiments, which tested mainly explicit monitoring, this experiment focuses on implicit monitoring—the ability to respond to errors in the absence of performance feedback.

The task used to assess error-monitoring is based on the original flankers task (Eriksen & Eriksen, 1974) that is often used in the error detection literature, with several modifications. First, we used shapes rather than letters as stimuli to remove the linguistic component of the task (Kopp & Rist, 1999). The patients were presented with equilateral triangles that could "point" upwards or downwards. Secondly, the stimuli were presented in a vertical array so that they could be presented within one visual field. Additionally, the flanking distractors were presented just before the target shape. This temporal offset has been shown to increase the distracting effect of the flankers (Flowers, 1990), leading to more errors.

METHOD

Participants. Two patients with complete cerebral commissurotomy participated in this experiment. Both patients underwent the surgery for treatment of intractable epilepsy. The first patient, N.G., was a 68-year-old female who was 30 years old at the time of her surgery. The second, A.A., was a 51-year-old male who was 14 at the age of surgery. Both patients underwent a complete single-stage midline section of the corpus callosum, anterior commissure, massa intermedia, and hippocampal commissure. Both patients were right-handed and had no major cerebral damage aside from the surgical section (Clarke & Zaidel, 1989). Recent MRI on both patients conducted in March 2002 confirmed the absence of the commissural fibers (L. Aziz-Zadeh, personal communication).

Procedure. The chinrest and computer setup was the same as the other experiments. The stimuli were black equilateral triangles, each side measuring .75° of visual angle. Two types of triangles were used: "down" pointing triangles had a flat edge on top, with a point at the bottom. "Up" triangles were flipped so that the pointed end faced upwards. Triangles were presented on a gray background, with their inner edge 1.5° of visual angle from the central fixation cross. Each trial began with two distractor triangles appearing either in the LVF or RVF. One triangle was above the midline, while the other was below, both in the same visual field. The triangles were positioned so that their edges were 1.5° above or below the horizontal midline. After 100 ms, the target triangle appeared between these two, on the horizontal midline in the same visual field as the distractors. All three triangles remained for another 50 ms, and then disappeared (see Figure 26). On half the trials, the stimuli appeared in the LVF, and on half they appeared in the RVF. Half of the targets were pointing up, and half were pointing down. The flanking stimuli were either compatible, pointing in the same direction as the target, or incompatible, pointing in the opposite direction. The two flanking stimuli always pointed in the same direction as each other. Half of the trials were compatible, and half incompatible.

Subjects were instructed only to respond to the central triangle. Responses were made by pressing spatially compatible keys on a response box – the top button was pressed for "up" triangles, and the bottom button was pressed for "down" triangles. Subjects were instructed to respond as quickly as possible, and to correct their errors by pressing the appropriate key on the response box. For example, if the subject erroneously pressed the bottom button in response to an "up" triangle, he or she should press the top button upon noticing the error.

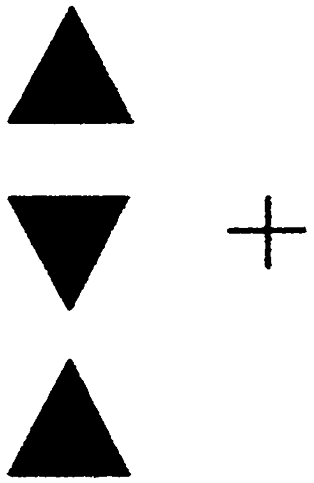


Figure 26: Stimuli from Experiment 8. Subjects respond to the direction of the central triangle.

N.G. first completed two blocks of 80 trials each. In the first block, responses were made with the right hand, and in the second responses were made with the left hand. Since her right hand/RVF trials showed no errors, we ran a third block in which she responded to RVF stimuli with her right hand, and to LVF stimuli with her left hand.

A.A. completed two blocks in which he responded to RVF stimuli with his right hand, and to LVF stimuli with his left hand.

RESULTS

In the first block, responding with her right hand, N.G. made no errors when the stimulus was in the RVF and 40% errors when it was in the LVF. In conditions where response hand and visual field of presentation are not the same, performance is expected to be poor. These "crossed" conditions require interhemisheric transfer. In the second block, when she responded with her left hand, she made 49% errors for LVF stimuli and 40% errors for RVF stimuli. Thus, her right hemisphere did not seem to be capable of performing the task. In the third block, which contained only "uncrossed" trials, she made 54% errors with her left hand/LVF and 35% errors with her right hand/RVF. N.G. did not correct any of her errors, despite repeated instructions to fix her mistakes.

A.A. completed two blocks with only uncrossed trials. With his left hand, he made 5% errors for compatible trials and 92% errors for incompatible trials. This suggests that A.A. was responding to the flankers rather than to the target. Instructions to respond only to the central triangle were repeated several times. With his right hand, he made 27% errors for compatible trials and 70% errors for incompatible trials. A.A. did not correct any of his errors.

DISCUSSION

Neither subject was able to self-correct in this task. N.G. had a difficult time performing the discrimination above chance with her right hemisphere. It is not surprising that she could not correct her mistakes if she could not tell what the right answer was. However, she made many mistakes with her left hemisphere in the third block that were not corrected. A.A. either believed he was supposed to respond to the flankers, or was so distracted by them that he could not help responding to them. Even if he thought the task was to respond to the flankers, he still made mistakes that went uncorrected. A.A. claimed to understand that he was supposed to correct his mistakes, and when asked after the experiment if he made any mistakes, he reported that he couldn't tell.

There are several possible explanations of these results. First, the patients simply may not have understood the error correction instructions. This is possible. Nevertheless, both patients were able to repeat the instructions back to the experimenter. Alternatively, they may have had low confidence in their ability to tell the right answer in the task.

A third explanation is that error detection requires interhemispheric interaction. As discussed earlier, one way that error correction might be accomplished is by two simultaneous parallel computations, the results of which are compared. If the two computations come up with the same answer, then this results in confidence in the answer. In the split brain, the results of left hemisphere processing and right hemisphere processing cannot be compared, resulting in diminished error detection.

Experiment 9: fMRI of feedback processing

The behavioral experiments with normal subjects have a supported a right hemisphere specialization for feedback processing in lexical decision. A key principle in cognitive neuroscience involves using evidence from converging methodologies so that the weaknesses of one technique are supported by the strengths of another. Using functional magnetic resonance imaging (fMRI) to measure blood oxygen level dependent (BOLD) responses in the brain allowed us to investigate the anatomical localization of the various functional processes involved in action monitoring. Specifically, lateralized changes in blood flow were expected in response to feedback processing.

This experiment is designed to compare activity of the brain when it is receiving performance feedback and when it is not. In an adaptation of the behavioral feedback paradigm, subjects in the scanner decided if what they had seen is a real word or not, and received meaningful or neutral feedback presented in the RVF or LVF. The stimuli were lateralized to allow testing of each hemisphere's response to feedback independently.

METHOD

Subjects. 12 graduate and undergraduate students were recruited from the UCLA population, half male and half female. Again, only right-handed native English speakers were tested. Subjects were screened to rule out a history of neurological or psychiatric disorders, substance abuse, or other medical conditions prior to scanning. The screening process also excluded anyone with metal anywhere in his or her body for MRI safety.

Materials and Procedure. A list of 3,4,5, and 6 letter string pairs consisting of 64 English nouns and 64 pronounceable nonwords was adapted from the earlier behavioral experiments. Words were counterbalanced for spelling-sound regularity and for frequency. In the task, one string is flashed in the LVF and another simultaneously in the RVF. One string is underlined to indicate the target; the other string serves as a distractor.

Anatomical and functional images were acquired using a GE 3.0T MRI scanner with an upgrade for Advanced Nuclear Magnetic Resonance-Echo Planar Imaging (ANMR-EPI) at the UCLA Brain Mapping Center. The subject was placed in the scanner wearing a pair of magnet-compatible goggles connected to a Macintosh computer controlled by MacProbe.

Before functional scanning, anatomical data were acquired for registration purposes with a coplanar high-resolution T2-weighted echo planar imaging volume. The parameters of this scan were as follows: TR = 4000ms, TE = 54ms, flip angle = 90°, 128x128 voxel matrix, 26 axial slices, 3.125mm in-plane resolution, 4mm thickness, 1mm spacing. Subjects were given a practice block of 24 trials in the scanner before functional imaging data acquisition began.

Subjects were instructed to keep their eyes focused on a fixation cross in the center of the screen throughout the experiment. Letter strings were presented on the screen for 150 ms in lower-case black letters on a gray background. On each trial, one string was presented in the LVF and one in the RVF, with one string underlined to indicate the target. Subjects were instructed to decide if the target string was a real word or not and respond as quickly and accurately as possible by pressing special response keys with the right hand. Following each response, a feedback signal was presented for 150 ms in the same visual field where the target had appeared. The feedback signals consisted once again of solid colored squares. Three colors were used, just as in the behavioral experiments. Again, a black square serves as the control/neutral stimulus. Participants were told that the black square does not provide any information about their performance. A blue square and a yellow square served as the meaningful feedback. For half of the subjects, a yellow square indicated a correct response and a blue square indicated an error. For the other half of the subjects, the colors were reversed.

There were four experimental conditions. In one condition, target letter strings always appeared in the LVF and were followed by meaningful feedback signals. A second condition presented stimuli in the LVF but subjects saw only a black, control stimulus after each trial. The third and fourth conditions involved targets presented in the RVF either with or without meaningful feedback. After an initial rest period of 44 seconds the experiment alternated between 32 second periods of task and 32 second periods of rest. Each task condition involved 16 trials lasting 2 seconds each. A full functional scan involved all four task conditions each separated by a rest period, for a total time of 5 minutes, during which 75 whole brain volumes were acquired. During rest periods, the subjects were instructed simply to look at the fixation cross. Each subject completed four full 5-minute functional scans, in which the order of conditions were counterbalanced.

Functional data were acquired using echo planar T2-weighted gradient echo sequence (TR = 4000ms, TE = 25ms, flip angle = 90°, 64x64 voxel matrix, 26 slices, 4mm thickness, 1mm spacing).

DATA ANALYSIS

One female subject was excluded from the analysis because of data corruption. Data analysis was accomplished using the Automated Image Registration software and involved the following steps:

1. Functional images for each subject were aligned with the corresponding anatomical co-planar high-resolution volume. This was done using a rigid-body linear registration algorithm (Woods, Grafton, Watson, Sicotte, & Mazziotta, 1998).

2. Images for each subject were spatially normalized into a common space. Each subject's images were warped into a Talairach-compatible brain magnetic resonance atlas (Woods, Dapretto, Sicotte, Toga, & Mazziotta, 1999) using fifth-order polynomial nonlinear warping (Woods et al., 1998).

3. Data were smoothed using an in-plane, Gaussian filter to produce a final image resolution of 8.7 mm by 8.7 mm by 8.6.

Statistical analysis were performed using t-tests (Woods, Iacoboni, Grafton, &

Mazziotta, 1996) on the sum of the signal intensity at each voxel throughout each task. The statistical threshold was set at $p = .001$ at each voxel. To prevent false positive, only clusters of 10 significant voxels were considered reliable activations.

RESULTS: BEHAVIORAL DATA

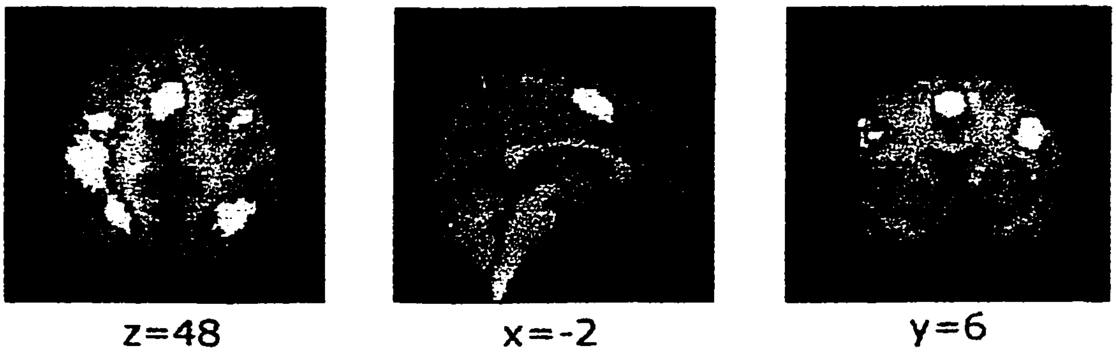
The behavioral data (latency and percent error) were subjected to a 2 (visual field: left, right) X 2 (wordness: word, nonword) X 2 (feedback: feedback, none) repeated measures ANOVA to look for the standard lexical decision effects. The difference between RVF targets (21% errors, 738 ms) and LVF targets (24% errors, 762 ms) was in the expected direction but did not reach significance. The difference between word targets (21.6% errors, 717 ms) and nonword targets (33.6% errors, 783 ms) was only significant in the latency data ($F(1,10)=44.58, p < .0001$). The wordness by visual field interaction was marginally significant in the error data, $F(1,10)=3.91, p =.076$. Also in the error data was an indication of better performance in blocks without feedback (20.9% errors) compared with feedback blocks (24.1% errors), $F(1,10)=4.66, p = .056$.

To examine explicit monitoring effects, the left and right feedback blocks were analyzed with a 2 (block: left, right) X 2 (previous trial feedback: positive, negative) repeated measures ANOVA. The latency data showed a significant main effect of previous trial feedback type, $F(1,10)=16.57, p < .01$. Subjects were slower on trials following negative feedback (780 ms) than on trials following positive feedback (736 ms), but this effect did not interact with visual field of feedback presentation. This analysis also showed a significant main effect of block, with reaction times faster in RVF feedback blocks (740 ms) compared with LVF feedback blocks (776 ms) $F(1,10)=9.44, p < .05$.

RESULTS: FUNCTIONAL IMAGING DATA

Task minus Rest. This contrast examined those brain areas that were more active in the task periods than in the rest periods to find brain activity associated with the lexical decision task. There were widespread activations associated with the task periods, including pre-motor areas bilaterally, supplementary motor areas bilaterally, primary motor cortex on the left side, and the frontal operculum on both sides. Also active were the inferior parietal lobule bilaterally, a temporal-occipital region on the left side, the precuneus bilaterally, and the cerebellum bilaterally. Some of these activations are depicted in Figure 27.

Figure 27: Brain regions significantly more activated in task conditions compared with rest conditions.


z=48 x=-2 y=6

Left Task minus Right Task. This contrast examined brain regions that were more active during LVF blocks compared to RVF blocks. There were no significant activations in this comparison, thus there was no evidence of any increased activity associated with LVF targets compared with RVF targets.

Right Task minus Left Task. This contrast examined brain regions that were more active during RVF blocks compared to LVF blocks. Significant activations were found in the left frontal operculum (Broca's area, see Figure 28), the left lingual gyrus, the right middle frontal gyrus, the left fusiform gyrus, and the right cerebellum.

Figure 28: RVF blocks minus LVF blocks. Activation in the left inferior frontal gyrus, pars opercularis.

z=12 x=-48 y=13

Feedback minus No-feedback. This contrast examined brain regions that were more activated during feedback conditions than conditions in which neutral feedback was presented. Several brain regions were found to be significantly more active when subject were receiving meaningful feedback (see Table 2). There were bilateral activations in the supplementary motor area and the precentral gyrus. Additional activations were found in the right postcentral gyrus, the left superior parietal lobule, the left cuneus, the right precuneus, and the left amygdala. These activations are depicted in Figure 29.

Table 2: Feedback minus no-feedback activations

Location	Side	Talaraich X	Talaraich Y	Talaraich Z	Brodmann's Area
SMA proper	L, R	-1	-23.3	66	6
Precentral gyrus	L	26	-16.6	64	6
Precentral gyrus	R	-18	-13.7	64	6
Postcentral gyrus	R	27	-39.5	64	5
Superior parietal lobule	L	-42	-61.5	50	7
Precuneus	L	-12	-76.8	50	7
Cuneus	R	9	-72.9	18	18
Fusiform gyrus	L	-30	-59	-13	19
Amygdala	L	-27	-7	-12	

No-feedback minus Feedback. This contrast shows brain regions that were more active in the blocks with neutral feedback compared with feedback blocks. No significant activations were found.

Right Feedback minus Right No-feedback. and *Left Feedback minus Left No-feedback.* These contrasts examined feedback effects within each visual field. No significant effects were found. This null result is probably due to the reduced power of this analysis compared with the one that includes both visual field blocks. Restricting the analysis to left or right visual field blocks halves the number of observations.

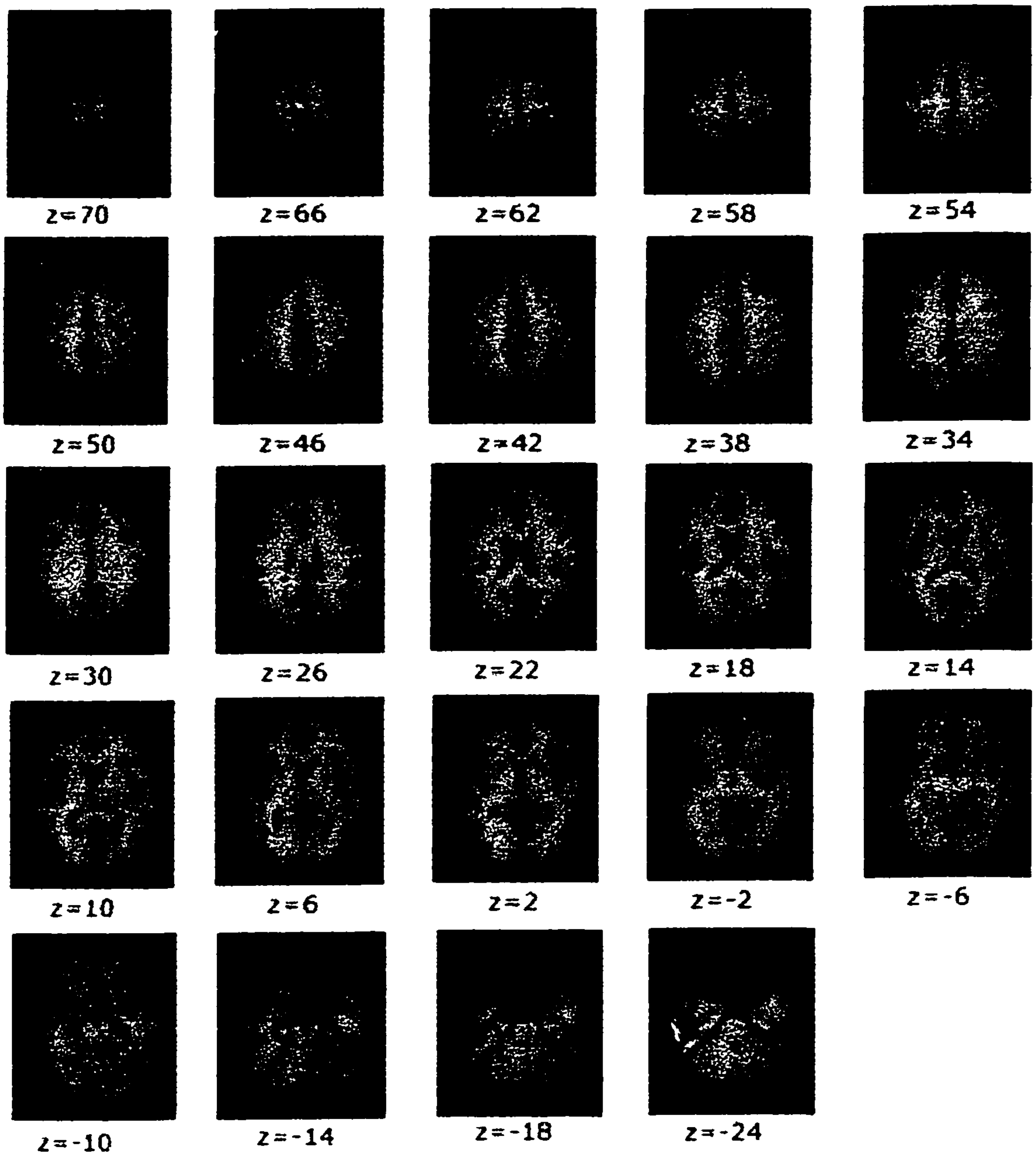


Figure 29: Brain regions significantly more active in feedback conditions compared with no-feedback conditions

DISCUSSION

The behavioral effects in the fMRI version of the lexical decision task were weak, but in the expected direction. Activations associated with the lexical decision task compared with resting baseline showed strong activations in motor planning and execution areas (Picard & Strick, 2001), visual areas, and areas known to be involved in word processing (Kiehl et al., 1999; Rumsey et al., 1997). However, this is not the cleanest test of brain regions involved in lexical processing, since the rest condition does not control for many aspects of the task. The experiment was designed specifically to compare blocks with feedback to those without feedback.

Nevertheless, comparisons between blocks with LVF targets and RVF targets yielded an interesting result. Several areas including the left frontal operculum were more active in RVF feedback blocks, but there were no corresponding right hemisphere regions that were more active in LVF blocks. These comparisons show that a common set of brain regions was activated by RVF and LVF stimuli, with the exception of some regions that were more active with RVF stimuli. This could be interpreted as evidence of a greater left hemisphere involvement in the task regardless of visual field of presentation (i.e. the callosal relay model (Zaidel et al., 1990)). In this scenario, LVF stimuli are shuttled across the corpus callosum from the right hemisphere to the left for processing. RVF stimuli can be processed directly in the left hemisphere without signal-degrading callosal transfer, thus yielding a stronger activation in RVF blocks. The region of the inferior frontal gyrus that was more active in RVF blocks has been found to be specifically involved in lexical processing, showing word-frequency dependent activations in a recent fMRI study (Fiebach, Friederici, & von Cramon, 2002).

The presence of feedback was related to an increase in error rate, and a post-error slowdown, indicating that subjects were sensitive to the feedback. Feedback blocks compared with no-feedback blocks showed several significant activations. First, there were activations in lateral and medial frontal motor regions, suggesting that the feedback led to a modulation of motor preparation processes. Cohen, Botvinick, and Carter (2000) have proposed that there are two mechanisms of control that may be elicited when the anterior cingulate system detects response conflict. The first involves attentional mechanisms controlled by the lateral prefrontal cortex. However, patients with lateral prefrontal lesions still show a post-error slowing, indicating that there is a second mechanism that does not rely on the prefrontal cortex. Cohen et al. suggest that this second mechanism may involve direct connections between the cingulate and motor preparation areas that can modulate response thresholds. The feedback information, then, may trigger control mechanisms that directly effect response preparation.

Feedback-related activations were also found in the left superior parietal lobule. The superior parietal lobule (SPL) has strong connections to the dorsal premotor cortex (Caminiti et al., 1999; Wise, Boussaoud, Johnson, & Caminiti, 1997), and may be directly involved in using visual information to guide movements. The dorsal premotor cortex/ SPL network has been implicated in the selection of motor responses based on visual cues. For example, a PET study by Grafton, Fagg, and Arbib (1998) found activation in these regions when a colored light indicated to subjects which grip they should use to grasp an object. Dassonville et al. (1998) recorded activity in SPL along with other motor regions when subjects made finger movements in response to unpredictable visual cues. Consistent with the present finding, in that study the SPL activity was found in the hemisphere contralateral to the response hand. Visual feedback, then, may be directly influencing response selection via the parietal lobe. This fronto-parietal network seems to be key for using visual information to inform action production.

The left amygdala was also more active in feedback blocks than in no-feedback blocks. This may represent an emotional reaction to the feedback. The amygdala is involved in predicting rewards (Schultz, 1998; Schultz, Tremblay, & Hollerman, 1998) and learning stimulus-reward contingencies (Everitt, Morris, O'Brien, & Robbins, 1991). In fact, a recent fMRI study showed amygdala activity in relation to positive and negative feedback in a simple reaction time task (Zalla et al., 2000). In this experiment, subjects responded as quickly as they could to a visual signal and then received linguistic feedback (i.e. the word "WIN" or "LOSE") that was not actually related to their response time. Several blocks were run in which the experimenters manipulated the proportion of positive and negative feedback. Activity in the left amygdala increased with an increasing proportion of positive feedback trials, while activity in the right amygdala increased with more negative feedback. In our lexical decision task, subjects perform close to 80% accuracy and so received mostly positive feedback. The left amygdala activation is likely related to the rewarding nature of the positive feedback stimuli.

Several other areas showed feedback-related activity, including the left precuneus, the left fusiform gyrus, and an extrastriate visual area on the right side. Paulus et al. (2002) found increased precuneus activation in a decision-making task associated with conditions with high error-rates. This suggests the precuneus may be involved in error detection or compensation, but its functional role is not clear. The activitiy in the fusiform gyrus corresponds closely to the coordinates of the V4 complex (Bartels & Zeki, 2000; Nunn et al., 2002). The feedback stimuli were blue and yellow compared with the black neutral feedback, so activity in V4 is not surprising.

Based on the results from the behavioral experiments, we expected to find right hemisphere activations associated with feedback, indicating a right hemisphere monitoring advantage. Instead, we found no activations related to the laterality of the feedback stimuli. Behavioral feedback effects in the previous studies were small, emerging with large numbers of subjects, and so this null result could relate to the subtlety of these effects. Behaviorally, subjects responded faster in the RVF feedback blocks compared with left feedback blocks, but since responses are faster overall to RVF stimuli this effect is not related to the presence of feedback. The network of activations elicited by the feedback stimuli was if anything lateralized to the left hemisphere. This is probably due to the fact that subjects were responding with their right hands. Most of the feedback-related activity was in sensorimotor integration regions specifically related to response preparation, and so the laterality is likely to reflect the response hand.

We did not find feedback-related activations in the anterior cingulate cortex, or in the dorsolateral prefrontal cortex. There is increasing evidence that this system responds specifically to negative events (Gehring & Willoughby, 2002). The feedback blocks in this experiment contained both positive and negative feedback, with mostly positive feedback due to the relative infrequency of errors. Instead of finding regions that react to negative events, we found brain regions that respond to reward, namely the left amygdala. To isolate the laterality of error monitoring networks, an event-related design would be necessary. In an event-related fMRI design we would be able to isolate the hemodynamic response to negative feedback compared with positive or neutral feedback. In the previous behavioral experiments there were two types of feedback effects examined that interacted with visual field. The first was a block effect, where LVF and RVF feedback blocks often differed. The second was a previous trial effect, which found that negative feedback had a different effect on the next trial depending on its visual field of presentation. The block effect was only present in the first lexical decision experiment with a between-subjects design. The other experiments only found the previous trial effect, indicating that hemispheric differences in self-monitoring may be specifically related to how the hemispheres handle failure. Since this experiment did not allow us to isolate the neural networks associated with failure specifically, it did not show lateralized activations consistent with a right hemisphere monitoring advantage.

In summary, this experiment shows that performance-related feedback invokes neural networks involved in sensorimotor integration and reward processing. Behavioral adjustments in response to feedback seem to be mediated by direct modulation of response programming mechanisms.

General Discussion

The series of experiments presented here provides new information regarding hemispheric specialization for executive monitoring, and raises several important new questions. Here I will summarize the data and synthesize the findings into several key themes. Table 3 summarizes the results of the behavioral experiments.

Table 3: Summary of feedback effects in the behavioral experiments

[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
1	Lex Dec, Faces	LVF	LVF	N/A	None
2	Lex Dec, Squares	None	LVF	RVF	None
3	Lex Dec, Words	None	None	None	None/RVF
4	Lex Dec, Arrows	None	None/LVF	None	None
5	Lex Dec, False feedback	None	F: LVF, M: RVF	None	F: None, M: LVF
6	Lex Dec, Opposite VF	None	None	LVF	None
7	Object Decision	RVF	None	RVF	None

This table shows the four feedback effects for each experiment. The "global" column represents whether a significant difference was found between blocks, and if so, which block was most sensitive to feedback. The "local" column shows whether negative feedback affected the next trial depending on visual field of presentation. The visual field which produced the best performance on the following trial is entered in the table. The Both column tells which visual field of feedback presentation led to the better performance in the Both blocks. The Implicit column represents an effect of errors on the next trial in the Control blocks, wherein only neutral feedback was presented. The white blocks did not show a significant effect. The gray blocks represent an effect that approached significance. The orange/vertical striped blocks are effects that indicate a LVF sensitivity to feedback, and the green/diagonal striped blocks indicate a RVF sensitivity. The blue/horizontal striped blocks showed a sex difference.

HEMIPSHERIC SENSITIVITY TO MODE OF FEEDBACK

The first four experiments in this dissertation found that the right hemisphere was more sensitive to performance feedback than the left in a lexical decision task, but that this sensitivity depends on the type of feedback stimulus. The strongest effect was found in the faces experiment. A right hemisphere monitoring advantage was also evident with colored squares as feedback, but was very weak with spatially coded feedback stimuli and disappeared with linguistic feedback. At the very least this pattern indicates that not all feedback is equal. In all four experiments, the same information was provided in the feedback stimulus: your response was correct, or it was incorrect. Subjects clearly recognized the difference between the two stimuli in all cases. However, different types of lateralized feedback stimuli produced different reactions.

One explanation for the particular pattern we observed is that the right hemisphere monitoring advantage is most pronounced when the feedback is presented in a mode easily understandable by the that hemisphere. The faces may have been particularly effective feedback stimuli because the right hemisphere processed them quickly and easily. However, we expected that the arrows, a spatially encoded signal, would fit well with right hemisphere processing style and produce a strong feedback effect, but this result was not found.

An alternative explanation for the enhanced effect of the facial stimuli concerns their emotional expressiveness. In these stimuli, the performance information was conveyed via a facial expression. The perception of facial emotions involves the amygdala (Iidaka et al., 2001; Kesler/West et al., 2001), an area we found to be activated by feedback stimuli in our fMRI study. If these feedback stimuli were more effective in activating limbic systems involved in assessing the reward value of the stimulus, then they would be expected to produce a stronger feedback effect than the emotionally neutral stimuli.

Still, the verbal stimuli and the arrows were less effective than the colored squares. Among these stimuli, the colored squares could be said to require the least amount of processing. The information is immediately perceptually apparent and does not require any lexical or spatial processing. The results of the fMRI study showed that a sensorimotor integration network was involved in mediating the effects of feedback. If the feedback stimulus can be processed with minimal decoding, the sensory information could be easily used to directly modulate response mechanisms.

A further difference between the faces experiment and the others concerns its between-subjects design. In the faces experiment, subjects in the experimental group completed only LVF and RVF feedback blocks, and never participated in a no-feedback block. In the other experiments, each subject completed four blocks each: a control block with no feedback, a LVF feedback block, a RVF feedback block, and a mixed feedback block. To the extent that there are long-lasting effects of the feedback stimuli, this methodological difference between the experiments could be significant.

GLOBAL VS. LOCAL FEEDBACK EFFECTS

There is evidence of both long-lasting and short-term effects of feedback in these experiments. Our analyses examined trials following negative feedback because these trials have been shown to reflect error-monitoring processes. Indeed, almost all of the experiments showed a "local" effect of negative feedback on the following trial, and these effects differed depending on the visual field in which the feedback was presented. However, in lexical decision the effects of negative feedback usually did not show up in the mixed feedback blocks, where feedback was presented after every trial and was not restricted to one visual field at a time. This suggests that the processing of each trial is not affected only by the previous trial, but also by the other trials within the same block, a "global" effect. This is to be expected if feedback induces long-lasting changes in attention or in processing strategy. This is in fact what we would predict based on the error-monitoring model outlined in the introduction. If the ACC/prefrontal network recognizes that a negative event has occurred, it should invoke the Supervisory Attentional System to readjust resources (i.e. attention) and exert executive control.

The fact that feedback effects only showed up when feedback was blocked by visual field (as opposed to when both visual fields received feedback within one block) may reflect an attentional shift during those blocks towards the visual field which was receiving feedback. This is supported by the indication that performance declined in the visual field that was not receiving feedback in most of these experiments. Subjects also reported paying attention to the visual field that was receiving feedback. In mixed blocks attention remained divided across the two visual fields and the feedback effects were not evident.

Further indication of an attentional factor that interacts with feedback processing comes from Experiment 6, in which feedback was presented opposite the lexical target. In this experiment, feedback had no local effect in the LVF and RVF blocks, but did have a local effect in the mixed block. Since feedback processing and target processing were separated in this experiment, the block that promoted divided attention facilitated feedback processing. In the other experiments, with the feedback and target stimulus in the same visual field, conditions that promoted the direction of attention to one side led to increased feedback effects. In other words, when feedback is blocked, attention is focused on one visual field, a condition which optimizes feedback processing as long as that visual field is receiving both target and feedback stimulus. When feedback is mixed, attention is spread across the two visual fields, a condition which generally lessens the impact of feedback processing, unless the target and feedback stimulus are sent to separate hemispheres.

Interestingly, Experiment 7, the object classification task, showed a local effect of type of feedback in the mixed feedback blocks but not in the separated blocks. Feedback processing in this task seems to benefit from the divided attention condition. Since we found a left hemisphere feedback sensitivity in this task, it could be argued that feedback processing in each hemisphere interacts differently with attention. When the right hemisphere is in charge of monitoring, feedback is processed best when attention is focused on one visual field, but when the left hemisphere is doing the monitoring, feedback is processed best in a situation with distributed attention.

Global effects of hemispheric feedback processing were examined by comparing performance among the four different feedback blocks: blocks with only neutral feedback, blocks with only LVF feedback, blocks with only RVF feedback, and mixed blocks. These effects turned out to be more elusive than the local effects, only appearing in Experiment 1 with facial feedback, Experiment 7, the object classification experiment, and to some degree in the fMRI experiment. As mentioned above, Experiment 1 had the advantage of isolating feedback blocks with a between-subjects design, which eliminates any carryover effects from the control and mixed blocks that subjects performed in the other experiments.

Since global and local effects did not always co-occur, we have evidence that they reflect different mechanisms. The only global effects we found in a within-subjects design was in the object decision experiment, where presenting feedback to the left hemisphere led to a global strategy adjustment within the block. In that same experiment, there was a local effect of feedback presented to the right hemisphere. The right hemisphere, then, may be more responsible for the local effects of feedback, while the left hemisphere mediates the global effects. The local effects of feedback may result from an error-detection response generated by the anterior cingulate in the right hemisphere. We have seen that the ACC tends to be larger on the right side (Watkins et al., 2001). The global effects, on the other hand, may reflect the results of left hemisphere control processes that adjust strategies and shift attention. In fact, the fMRI data speak directly to the basis of the global effect, since this experiment used a blocked design to compare brain activity in feedback blocks to non-feedback blocks. These data suggest that the global effects of feedback mediate thresholds for motor responses in neural motor planning networks in the left hemisphere.

This does not mean that local and global effects are entirely independent. It may be that local effects build over time to produce global effects provided that there is a consistent local effect happening within the block.

IMPLICIT VS. EXPLICIT MONITORING

Implicit monitoring involves recognizing that an error has been made in the absence of explicit performance feedback. In most of these experiments, when the neutral feedback blocks were examined, there was no evidence of implicit monitoring. We generally did not find that subjects tended to slow down following their errors. The most likely reason for this effect is the separation of one trial from the next by the neutral feedback stimulus.

However, there was a key situation in which implicit monitoring effects did show up. In Experiment 5, when the explicit feedback was false, male subjects showed implicit monitoring in the control blocks. This tells us that it is possible to find evidence of implicit monitoring on the next trial even in the presence of the intervening neutral feedback stimulus. In this experiment males did not react to the explicit feedback in the same way they did in other experiments. Thus, there is an interaction between implicit and explicit monitoring. At least for males, the fact that they are receiving feedback does not cause them to stop monitoring on their own. On the contrary, they continue to monitor and compare their internal error monitoring to the external feedback. When they realized the discrepancy, they focused more on the implicit monitoring enough that we started to see error-related effect in the control blocks. The direction of this implicit monitoring effect was consistent with the one found by Iacoboni, Rayman, and Zaidel (1997), with better performance following LVF errors.

For explicit monitoring, we found a right hemisphere superiority in the lexical decision, but a left hemisphere superiority in the object decision task. Does implicit monitoring follow the same pattern? The only time implicit monitoring did show up in lexical decision (in the males in Experiment 5) it did indicate better performance after LVF errors. However, there is no corresponding evidence of implicit monitoring in the object decision task to make a comparison. An avenue for future research would be to examine previous trial effect in object decision without the neutral feedback stimulus. The evidence from the split-brain patients on implicit monitoring was inconclusive. If anything, these data showed that interhemispheric cooperation is necessary for error detection. One hemisphere cannot self-monitor on its own, perhaps because parallel computations in the two hemispheres need to be compared in order to detect errors.

COGNITIVE LOCUS OF FEEDBACK EFFECTS

What is the cognitive locus of the feedback effects that we observed in these experiments? In other words, what stage of processing does performance feedback affect?

There are several indications about the answer to this question. Derryberry (1990) argued that lateralized feedback works at a motor or premotor level. He found that stimulus-response compatibility interacted with the feedback effect. Derryberry reasoned that feedback changes the way that sensory and motor systems interact. This is precisely what the data from our fMRI study suggest. We found that in feedback conditions there was increased activity in sensorimotor integration networks in the brain. It is as if the sensory feedback is being used to adjust response tendencies (Cohen et al., 2000).

Experiment 1 found that in LVF feedback blocks, there was an altered wordness by visual field interaction. The standard pattern shows a word advantage only in the LVF. However, in this feedback condition, there was a wordness advantage in both visual fields. This could be explained by a shift in response biases in the feedback blocks. A similar effect was found in the object decision task, where RVF feedback modulated the visual field by possibility effect. These effects are interesting because they interact with visual field. This means that the feedback-induced adjustment in response bias is not symmetrical.

HEMISPHERIC DYNAMICS IN FEEDBACK PROCESSING

The goal of this research was to understand how executive functions are handled differently by the two cerebral hemispheres, which are taken to be examples of semi-independent cognitive modules. Does the brain have one central monitor or do the two hemispheres do their own monitoring? If there are separate monitors in the two hemispheres, how are they different and how do they interact? This research has shown evidence of both hemispheric independence and hemispheric interaction in feedback processing.

First, the data presented here show that rather than one integrated, general-purpose executive monitor, the brain has several systems involved in responding to errors and performance feedback. The finding that feedback induced different behavioral responses depending the visual hemifield in which it was presented is strong evidence that the two hemispheres have independent monitoring and control mechanisms. For example, in Experiment 1, feedback led to an increase in performance when it was presented to the right hemisphere, but a decrease in performance when presented to the left hemisphere. If there were only one central monitor, we would expect similar reactions to LVF and RVF feedback.

Furthermore, we found that one hemisphere is not specialized overall for monitoring. That is, a central monitoring mechanism does not exist within one hemisphere. If one hemisphere was specialized to be an all-purpose monitor, we would expect to find that feedback was always more effective when presented to that hemisphere. The effects of feedback would be attenuated when feedback was presented to the non-specialized hemisphere because of callosal transfer. The data show a much more complex pattern, suggesting at least partial independence of hemispheric monitoring functions. First of all, sometimes feedback produced an opposite effect depending on the visual field of presentation. Secondly, the effects of feedback were different depending on hemispheric specialization for the task to be monitored. We did not find the same effect of feedback in the object classification task as we did in lexical decision.

We also found that in order for feedback to be processed effectively, it must be presented to the same hemisphere which computed the initial decision. This can be interpreted as additional evidence for hemispheric independence of executive functions, since it seems to imply a lack of interhemispheric collaboration.

The context effects are further evidence of the complexity and diversity of the neural systems involved in feedback processing. Blocked feedback conditions were different from mixed feedback conditions, and these effects varied from experiment to experiment. This suggests that there is a complex interaction between attention, hemispheric specialization, and self-monitoring. Also, the systems responsible for the subject's immediate reaction to a negative feedback stimulus may not be the same systems that adjust attentional resources and task strategies. The picture emerging is of a decentralized network of neural systems that accomplish the various functions associated with metacognition.

In addition to hemispheric independence, there also seems to be significant interhemispheric interaction necessary for self-monitoring. Split-brain patients were unable to correct their errors, which could indicate that interhemispheric communication is necessary for implicit monitoring.

Also, since feedback processing changed from task to task, there must be some way for monitoring functions to be allocated depending on the current demands. The left hemisphere was better at making lexical decisions, but the right was better able to use feedback productively in that task. The right hemisphere was better at making object decisions, but did not react to feedback in that experiment. This pattern could mean that hemispheric specialization directly interacts with monitoring ability, and that the two hemispheres trade processing and monitoring roles dynamically. The allocation of monitoring functions might involve one hemisphere inhibiting the executive processes of the other.

Conclusions

This dissertation shows that the two hemispheres of the human brain have distinct reactions to performance feedback in different situations and accomplish monitoring through a combination of cooperation and independent processing. Hemispheric specialization for self-monitoring depends on the nature of the feedback stimulus and on the type of cognitive operation being monitored.

Additionally, feedback processing leads to activation of neural systems related to emotional evaluation and sensorimotor integration that can directly affect response selection. However, there may be different mechanisms that underlie local and global reactions to feedback. Taken together, the data described here provide evidence of a distributed, decentralized, dynamic neural system for metacognitive processing.

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