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The cost of action miscues: Hemispheric asymmetries

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ABSTRACT

Adaptive behaviors require preparation and when necessary inhibition or alteration of actions. The right hemisphere has been posited to be dominant for preparatory motor activation. This experiment was designed to learn if there are hemispheric asymmetries in the control of altered plans of actions. Cues, both valid and invalid, which indicate the hand most likely to be called onto respond, as well as the imperative stimuli that indicate the actual response hand, were presented to either the right or left visual fields of 14 normal right handed participants. The delay after a miscue is dependent on the time taken to inhibit the premotor and motor systems of the incorrectly activated hemisphere, as well as to activate the motor systems of the opposite hemisphere, which might have been interhemispherically inhibited by this miscue. Analyses of reaction times revealed that miscues presented in left hemispace (right hemisphere) cost more time than those miscues presented in right hemispace (left hemisphere), suggesting that activation of the preparatory systems controlled by the right hemisphere may take longer to reverse than those controlled by the left hemisphere. This asymmetry may be related to asymmetries in the strength of hemispheric activation with contralateral inhibition.

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1. Introduction

A person prepares to act based on environmental contingencies. This preparation often enhances the efficiency of actions. Environmental cues, however, can be misleading. Thus, adaptive behaviors may require that the action for which one has prepared to be withheld or altered.

Prior studies have suggested that the right hemisphere may be dominant for both preparatory motor activation and motor inhibition. In regard to preparatory motor activation or action intention, it has been repeatedly demonstrated that reaction times are more rapid when valid warning stimuli are presented prior to the imperative stimuli, than when there are no warning stimuli. Kornhuber and Deecke (1965) reported that prior to a voluntary movement there was a change in the medial frontal lobes' electrical activity. They called this activity the "Bereitschaftpotential" or readiness potential. Warning stimuli appear to increase the activity in both the medial (pre-supplementary motor area, the supplementary motor area) and the lateral premotor areas (Shibasaki & Hallett, 2006).

In regard to asymmetries of preparatory motor activation, Heilman and Van Den Abell (1979) provided normal subjects with lateralized visual cues as to the hand that most likely would be asked to be used in response to a midline imperative stimulus. They found that the cues presented in the left visual field and directed to the right hemisphere reduced reaction times, more than did cues presented to the left hemisphere. Thus, Heilman and Van Den Abell's experiment, as well as a subsequent study by Verfaellie, Bowers, and Heilman (1988), suggest that the right hemisphere is dominant for preparatory motor activation. Studies of brain injured subjects appear to further support the hypothesis that the right hemisphere is dominant for preparatory motor activation. For example, when equated for lesion size and location, patients with right hemisphere lesions have slower reaction times using their ipsilesional hands than those with left hemisphere lesions (Howes & Boller, 1975) and contralesional limb akinesia is more likely to be seen after right rather than left hemisphere lesions (Coslett & Heilman, 1989).

In regard to response inhibition, de Zubicaray, Andrew, Zelaya, Williams, and Dumanoir (2000) examined response inhibition using fMRI and noted increased regional activity in a distributed network in both cerebral hemispheres, but there was more extensive activation in the right hemisphere's prefrontal region. Similarly, Garavan, Ross, and Stein (1999), Konishi, Nakajima, Uchida, Sekihara, and Miyashita (1998); and Brass, Zysset, and von Cramon (2001) also showed that the right dorsolateral frontal lobe activates during response (motor) inhibition.

Studies of patients who have discrete lesions have provided converging evidence for the postulate that the right frontal lobe might be critical in motor inhibition. For example, Aron, Fletcher, Bullmore, Shahakian, & Robbins (2003) demonstrated that damage

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to the right prefrontal cortex impairs response inhibition; and Na and colleagues (1999) demonstrated that patients with right frontal disease, when using their right hands, had motor perseveration, a form of defective response inhibition where subjects cannot stop responding.

Other studies suggested that response inhibition is mediated by the medial portions of the frontal lobe. For example, Watanabe and colleagues (2002) studied normal subjects during a Go-No Go task and found bilateral medial frontal activation, but when Verfaellie and Heilman (1987) studied patients with left or right medial frontal lobe lesions, only the right medial lesion was associated with defective response inhibition.

Although behavioral, functional imaging, and lesion studies have suggested that the right hemisphere is dominant for response inhibition, it is unclear if an activated right hemisphere inhibits the left hemisphere motor systems more than an activated left hemisphere inhibits the right. Because the right hemisphere has been posited to be important for both preparatory motor activation and for motor inhibition, the goal of the present study was to learn if there are hemispheric asymmetries of motor inhibition in normal subjects by using a miscue reaction time paradigm.

The methods used to investigate motor response inhibition or preparatory motor activation are, in part, based on previous studies of attention. Posner and Cohen (1984) demonstrated that there is an initial facilitation of target detection immediately following the presentation of a cue. More recent efforts to investigate the allocation of attention have utilized a covert orienting paradigm and included both valid and invalid cues (Facoetti, 2001; Ro, Machado, Kanwisher, & Rafal, 2002). In this paradigm, spatial cues are typically presented just prior to the presentation of the target stimuli. In the valid condition, the target appears in the cued position. In the invalid condition, the target appears in the uncued position. In addition, Laarni (1999) compared the effect of color and location cues on the allocation of attention and demonstrated that both color cues and location cues influenced attention. In this current experiment, valid cues provide information about which hand was to be used to respond to an imperative stimulus while invalid cues might activate the premotor and motor systems of the hemisphere ipsilateral to the correct response hand. In this condition reaction times might be slowed because the incorrectly activated hemisphere might inhibit the motor systems of the opposite hemisphere. This cued hemisphere's activation, together with the inhibition of the contralateral hemisphere, must be reversed before the subject can respond with the correct hand. This experiment was designed to learn if there are hemispheric asymmetries of motor inhibition such that miscues directed to the right hemisphere induce a greater cost (reaction time slowing) or a reduced cost compared with those directed to the left hemisphere.

2. Methods

2.1. Research participants

Fourteen healthy college students participated (6 men, 8 women) in this experiment. Participants were all strongly right handed as determined by a modified version of the Annett (1967) handedness test. All participants had intact color vision, no history of head trauma or a neurological disorder, and normal or corrected-to-normal vision. Participants were also free of substance abuse and psychiatric diseases. Participants' ages ranged from 18 to 33 years and education ranged from 13 to 16 years. All participants gave written informed consent according to procedures established by the Health Center Institutional Review Board at the University of Florida.

2.2. Experimental task

Each participant was tested individually in a quiet laboratory. Participants were seated 16 in. in front of a 17-in. computer screen. The background color (dark blue) of the monitor screen was held constant. Each trial started with a small cross at the center of the monitor screen that was displayed for 1100 ms. The participants were asked to focus upon the cross that was displayed in the center of the screen. Prior the onset of the imperative stimulus (500 ms) there was a red or green square (approximately 1.5 cm) cueing stimulus presented for 300 ms. These cues were presented approximately 7 cm to the left or right of the fixation point. The cues were considered "valid cues" when the color of the cue stimulus was the same as the color of the subsequent imperative target stimulus and invalid when they did not match. The color of the subsequent imperative stimulus (red or green) instructed the subject as to which hand was to respond. Thus, the valid cues had subjects correctly prepare their right or left hand to respond and the invalid miscues had subjects prepare for an incorrect movement. The colored square imperative stimuli were also presented laterally approximately 7 cm to the right or left of the fixation point. The imperative stimuli remained present until the key was pressed. The spatial location of both cue and imperative stimuli (right or left of midline) was randomized.

The participants responded to the imperative target stimuli by pressing the "X" key on a standard keyboard (left side) with the left index finger for one color and the "." key (right side) with the right index finger for the other color. Half of the participants responded to red stimuli with the left hand and to the green stimuli with the right hand. The other half of the participants responded in the reverse order of this color-hand pairing. Overall, for each participant, 80% of the trials were valid cues and 20% of the trials were invalid miscues. Because we are investigating the cost of invalid cues delivered to either the right or left hemisphere we did not present uncued trials. The order of presentation of the valid verses invalid cues was randomized. Prior to the experimental trials, participants completed a series of practice trials until each participant reported comfort with the task.

3. Analysis and results

The means and standard deviations of miscue costs are provided in Table 1. Miscue cost was calculated (cost = invalid miscue reaction time − valid cue reaction time). This cost presumably represents the time it takes to reverse the incorrectly activated or inhibited hemisphere.

A three way univariate analysis of variance (ANOVA) was conducted on the dependent variable of cost. This ANOVA had the following conditions: Miscue-Field (right versus left), Imperative Target-Field (right versus left), and Hand (right versus left). This analysis revealed a significant main effect of Miscue-Field such that the cost was higher when the miscue was presented in left hemispace (to the right hemisphere) than in right hemispace (to the left hemisphere). There were also significant interactions between Miscue-Field and Imperative-Target-Field F

Table 1
Descriptive statistics for miscue costs.

	Mean	Standard deviation
Cost of Miscue-Field versus Target-Field		
Left Target-Field	72.34	37.75
Right Target-Field	62.81	39.78
Cost of Miscue-Field versus Hand		
Left Hand	64.26	41.03
Right Hand	70.88	38.97