

Does each hemisphere monitor the ongoing process in the contralateral one?

Eldad Yitzhak Hochman* and Zohar Eviatar

Department of Psychology and the Institute of Information Processing and Decision Making, University of Haifa, Haifa, Israel

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Abstract

The present study was conducted to examine hemispheric division of labor in the initial processing and error monitoring in tasks for which hemispheric specialization exists. We used lexical decision as a left hemisphere task and bargraph judgment as a right hemisphere task, and manipulated cognitive load. Participants had to respond to one of two stimuli presented to both visual fields and were instructed to correct their errors. To achieve enough correctable errors, participants were encouraged to respond quickly by using a bonus system. The results showed the classical asymmetry for initial responses in both tasks and reversed asymmetry for corrections in the bargraph task at both load conditions, and in the lexical decision task at the high load condition. The results suggest that each hemisphere monitors the ongoing process in the contralateral one and that the dissociation of initial process and its monitoring grows with load of task.

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1. Introduction

A large amount of research in the last 50 years has shown performance asymmetries in lateralized tasks that are interpreted as reflecting hemispheric specialization for the tasks being performed. However, relatively little is known about how the two hemispheres of the brain differ in their ability to detect and respond to errors in these same tasks. 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 1960s and 1970s Patrick Rabbitt and his colleagues conducted a series of behavioral experiments using the choice reaction time paradigm. They found that when participants made errors, they tended to slow down on the following trial. This post-error slowdown was interpreted as spontaneous self-monitoring in this task (Rabbitt, 1966a, 1966b; Rabbitt & Phillips, 1967; Rabbitt & Rodgers, 1977; Rabbitt & Vyas, 1970). Other experiments with choice reaction time tasks have also

shown that participants do often have explicit awareness of their errors. When allowed to correct their responses, participants do so on about 14% of the trials, while uncorrected errors are very rare, occurring only on about 1% of trials (Kopp & Rist, 1999).

Scheffers and Coles (2000) have argued that errors resulting from premature responding are more detectable than errors resulting from perceptual or cognitive limitations, because a monitoring system can 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. However, if an error is resulted from poor processing of the stimulus rather than by premature responding, how can the monitor ever know what the appropriate response should have been?

One possible answer to this was 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. He suggested that the two cerebral hemispheres constitute these modules. The consensus in the field of

* Corresponding author. Fax: +972-4-8249431.

E-mail address: ehochman@study.haifa.ac.il (E.Y. Hochman).

laterality is that the majority of cognitive functions are within the capabilities of both hemispheres, with asymmetries arising from the efficiency and the manner of performance, such that corresponding functional modules in the two hemispheres would be well suited for this type of monitoring. Zaidel, Clarke, and Suyenobu (1990) have argued that each hemisphere functions as an independent cognitive unit, complete with its own perceptual, motoric, and linguistic abilities. According to this view, it is possible that each hemisphere has its own independent executive control, including the ability to monitor errors and correct them. In addition, studies exploring interhemispheric interactions have shown that performance improves when operations are divided across the hemispheres (Hellige, Jonsson, & Michimata, 1988; Liederman, 1986; Luh & Levy, 1995). Thus, even though one hemisphere may do a particular task less capably or efficiently than the other, it nonetheless has the capacity to contribute (Beeman & Chiarello, 1998; Chabris & Kosslyn, 1998).

Banich and her colleagues have suggested that division of labor between the cerebral hemispheres occur when tasks are resource demanding (Banich & Belger, 1990; Banich & Karol, 1992). Hochman and Meiran (submitted) have shown that error monitoring cannot occur in an efficient manner at the same time as response selection, and thus consider it a resource consuming process. However, error monitoring is ubiquitous in models of higher cognitive processes and is hypothesized to occur concurrently with other cognitive mechanisms. Hence, it seems plausible to assume hemispheric dissociation between initial processing and subsequent error monitoring.

Zaidel's solution to the monitoring problem is the following: when tasks are not well learned the load on a given hemisphere is too heavy for a single hemisphere to do both initial processing and the error monitoring. Hence, for a given task, the hemisphere that is specialized for the task performs the initial computations and selects the response. Concurrently, the other hemisphere monitors performance (Zaidel, 1987). However, to date, there is no empirical evidence to support this claim.

Psychophysiological evidence for laterality patterns in error monitoring is not straightforward. Recent event-related potential (ERP) studies using choice reaction time paradigms have revealed a negative-going deflection in the EEG only on trials in which the participants made errors. This deflection is known as the error-related negativity (ERN) (Gehring, Goss, Coles, Meyer, & Donchin, 1993). It was suggested that the ERN reflects a neural system concerned with the detection and compensation for errors (Gehring, Coles, Meyer, & Donchin, 1995). However, it is not clear what the anatomical substrate for this system is. The poor spatial resolution of EEG does not allow for accurate localization, although the ERN seems to be stronger at frontal and central scalp electrodes. Dehaene, Posner,

and Tucker (1994) used source dipole localization techniques to estimate the source of the ERN and proposed that the lateral anterior cingulate gyrus (ACC) is a likely source. In their study the equivalent dipole was so close to the midline that they could not tell with any confidence whether it indicated left, right, or bilateral activation. Furthermore, when the data from left- and right-hand responses were examined separately, the topography of the ERN did not seem to be affected by the side of response. The ERN was always maximal on the midline and not on the side contralateral to the response hand.

Although the source of error-related negativity seems to be the ACC, which is too medial to allow laterality distinctions, there is reason to believe that the ACC monitoring system is not completely symmetrical. Anatomical asymmetries have been found both in the ACC itself (Ide et al., 1999; Paus, 2001; Watkins et al., 2001; Yucel et al., 2001), and in the entire frontal lobe (Watkins et al., 2001; Weinberger, Luchins, Morihisa, & Wyatt, 1982). In an event-related fMRI study of error processing, Kiehl, Liddle, and Hopfinger (2000) found ACC activity bilaterally and left lateral prefrontal activity associated with errors in a go/no-go task. Menon, Adelman, White, Glover, and Reiss (2001) also used fMRI to measure error-related neural activity in a go/no-go task but found activation in the right ACC 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 these data.

Few behavioral studies have specifically looked at hemispheric differences in error processing. Iacoboni, Rayman, and Zaidel (1997) investigated how the previous trial affects the current trial in a lateralized lexical decision task. They found that accuracy improved on left visual field (LVF) trials following errors, while performance on right visual field (RVF) trials following errors, was unaffected. An improvement after an 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 (RH) error processing advantage. Kaplan and Zaidel (2001) also looked at the effect of the previous trial on the current trial in a lateralized lexical decision task. However, they investigated each hemisphere's ability to respond to external feedback about its performance. Their study showed a RH advantage in reaction to feedback. Notice that by looking at effects of external feedback to the previous trial on the current trial, the issue of hemispheric differences in detecting errors is bypassed in favor of investigating differences in compensating for errors.

In the present study we looked for laterality patterns in spontaneous self-corrections (i.e., error detection and correction). We used a bargraph judgment task that consistently results in asymmetry in favor of the RH (Boles, 1994) and a lexical decision task, known to result in left hemisphere (LH) superiority (Bryden, 1982; Hellige, 1993), in a within subject design. We presumed that if each hemisphere monitor the ongoing process in the contralateral one as suggested by Zaidel (1987), then in visual half field presentation it is expected that for both the RH task and the LH task, classical asymmetry would be found for initial decisions, whereas a reversed asymmetry is expected for corrections. That is, for a given task, an advantage in responding to stimuli presented to the visual field (VF) of the superior hemisphere is expected for initial decisions, whereas, an advantage in responding to stimuli presented to the VF of the inferior hemisphere is expected for corrections. The rationale is that according to the dissociation presumption, when a stimulus is presented to the inferior hemisphere, the superior one does the monitoring and vice versa. Thus, an advantage of presentation to the VF of the inferior hemisphere is always expected for corrections.

In order to assume contralateral monitoring as an interpretation for reversed asymmetry in corrections, two substitute explanations must be eliminated. One possible explanation is that in tasks for which hemispheric specialization exists, the inferior hemisphere is more “willing” to replace an already given response in case of possible error than the superior one does. This could be due to its “lower obligation” toward its initial process. If that is the case then the inferior hemisphere should show more cases of false corrections, that is, more cases in which an initial correct response is replaced with an incorrect one, than the superior hemisphere. Another possibility is that error monitoring begins before the initial response is executed. Hence, because it takes longer for the inferior hemisphere to do the initial process, and because we measured correction reaction time (RT) from the execution of the initial response, then, in the inferior hemisphere much of the error processing was done before RT measurement began, resulting in shorter correction RTs in the inferior hemisphere than in the superior hemisphere. If that is the case then a correlation should be found between RTs of erroneous initial responses and RTs of subsequent corrections.

In addition, to test Zaidel’s claim for labor division between the hemispheres in error monitoring due to resource limitations, we manipulated task cognitive load between subjects, by comparing a condition in which stimulus-response mapping remains constant to a condition in which stimulus-response mapping changes frequently. We expected the reversed asymmetry for corrections to be stronger in the second condition.

2. Method

2.1. Participants

Participants were 50 native Hebrew speakers. Half participated in the low cognitive load condition and half participated in the high cognitive load condition. All were students at the University of Haifa. All of the participants were right handed, had no left-handed family members, and had no history of neurological illness. Each participated in both the bargraph and the lexical decision tasks.

2.2. Low cognitive load condition

2.2.1. Bargraph judgment task

2.2.1.1. Materials. The stimuli were six bargraphs representing whole numbers from 1 to 6 (Boles, 1994). The bargraphs appeared as vertical rectangles against horizontal reference lines at the 0, 4, and 8 levels. Each bargraph appeared 72 times in each VF resulting in 432 experimental trials. The bargraphs subtended $2.4^\circ \times 6.7^\circ$ off visual angle with the inner edge 2° from fixation. The center of the bargraphs was level with the fixation point. Each target bargraph was randomly paired with the others to form bilateral displays. A directional arrow appearing at fixation (< or >) indicated to the participant which VF contained the target stimulus in a random sequence. Thus, a stimulus display on each trial consisted of a directional arrow in the center and two bargraphs, one in each VF. The stimuli were composed of black lines on a gray background.

2.2.1.2. Procedure. The participants were seated with their chin in a chin rest that held their eyes 57 cm from the screen. The participants were asked to indicate whether the number represented by the target bargraph was odd or even by pressing one of two keys (ascending or descending arrow) with their index finger. The participants first performed a practice set of 40 trials, during which feedback was given about the correctness of the response (happy or sad face at the fixation). No feedback was given during the experimental trials. The participants were asked to respond as quickly and as accurately as possible. The participants were encouraged to spontaneously correct themselves if they thought they had made an error. In order to achieve enough correctable errors, a bonus system was administered giving full credit for quick correct responses and a quarter of a credit for delayed responses (indicated by a sound) or corrections. The sequence of events on each trial was as follows: A 1000 Hz tone sounded for 100 ms to alert the participant that the trial was beginning, the fixation cross was presented alone for 100 ms, immediately the stimuli were presented for 90 ms. After the stimuli

disappeared the participant was given 3400 ms to respond (initial response and a correction if needed). The next trial began after 2 s. In case no response was given 900 ms after the stimuli disappeared, a short sound was presented, indicating delayed response. The experimental trials were presented in six blocks of 72. At the end of each block feedback was given indicating the number of credits earned, for quick, delayed, and correction responses. Between blocks the participants had to switch response hands.

2.2.2. Lexical decision task

2.2.2.1. Materials. The stimuli were two lists of 216 four-letter Hebrew words and 216 four-letter Hebrew pronounceable orthographically regular non-words. For each participant, each list was randomized and strings from one list were paired with strings from the other list to create 432 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 VF was counterbalanced across participants. Items that served as targets in one block served as distractors in the other block. Letter strings were presented in black letters on a gray background for 130 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. 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.

2.2.2.2. Procedure. As in the bargraph task except for the following: The participants were asked to indicate whether the underlined letter string was a word or a non-word.

2.3. High cognitive load condition

Tasks, materials, and procedure were as in Section 2.2 except for the following: The participants completed 24 blocks of 18 trials each. In each block, stimulus-response mapping was switched so that while responding in a given block, the participants had to inhibit the tendency to respond according to the mapping that was used in the previous blocks. In half of the blocks participants had to respond with their right hand and in the other half they had to respond with their left hand in a random order.

3. Results

All of the participants responded with above chance accuracy, the maximum error rate was 36% in all of the conditions.

3.1. Initial responses

The mean reaction times (in ms) for correct responses and error scores were subjected to a 3-way analysis of variance with cognitive load (low cognitive load vs. high cognitive load) as a between subject variable, and task (lexical decision vs. bargraph judgment) and VF (left vs. right) as within subject variables.

Corrections. The same analysis as above. Corrections RTs were measured from initial response to correction response. Correction error scores were calculated as the percentage of uncorrected initial erroneous responses out of total erroneous responses.

3.2. Initial decisions

For both reaction time and error scores the 3-way interaction between cognitive load, task, and VF was not significant. The main effect of cognitive load was significant [RT: $F(1, 48) = 9.34, p < .01$; error scores: $F(1, 48) = 10.01, p < .01$] revealing longer RTs ($M = 810$), and more errors ($M = 32\%$), in the high load condition than in the low load condition ($M = 780$ ms, $M = 24\%$). The interaction between task and VF was significant in both measures [RT: $F(1, 48) = 6.99, p < .05$; error scores, $F(1, 48) = 6.54, p < .05$].

Planned comparisons within each task revealed that in the bargraph task, the effect of VF was significant for RT [$F(1, 48) = 9.43, p < .01$] with faster correct responses to stimuli presented to the LVF (right hemisphere) ($M = 750$) than the RVF (left hemisphere) ($M = 808$). This effect was also found for errors, [$F(1, 48) = 6.97, p < .05$] with lower error percentage to stimuli presented to the LVF (right hemisphere) ($M = 22.2\%$) than the RVF (left hemisphere) ($M = 32.0\%$).

In the lexical decision task the main effect of visual field was also significant, in the opposite direction: For RT [$F(1, 48) = 8.76, p < .01$] with faster correct responses to stimuli presented to the RVF (left hemisphere) ($M = 776$) than the LVF (right hemisphere) ($M = 804$); and for errors [$F(1, 48) = 6.88, p < .05$] with lower error percentage to stimuli presented to the RVF (left hemisphere) ($M = 19.4\%$) than the LVF (right hemisphere) ($M = 27.1\%$).

No other effects in the overall analysis reached statistical significance.

Corrections. The mean RTs (in ms) for correct correction responses and error scores (calculated as the percentage of uncorrected initial erroneous responses out of total erroneous responses) were subjected to a 3-way analysis of variance with cognitive load (low cognitive load vs. high cognitive load) as a between subject variable, and task (lexical decision vs. bargraph judgment) and VF (left vs. right) as within subject variables.

A significant 3-way interaction between Cognitive Load, Task, and VF was found for corrections for both

RT and error scores [for RT: $F(1, 48) = 8.9, p < .01$; for errors: $F(1, 48) = 11.2, p < .01$].

3.3. Low cognitive load

In the bargraph task the main effect of visual field was significant in both RT [$F(1, 24) = 7.38, p < .05$] and in errors, [$F(1, 24) = 6.33, p < .05$]. As shown in Fig. 1, both measures reveal a significant RVF advantage, with faster and more accurate correction in the RVF (left hemisphere) (405 ms, 16.2% uncorrected initial erroneous responses) than the LVF (right hemisphere) (436 ms, 27.6% uncorrected initial erroneous responses).

In the lexical decision task the main effect of visual field was not significant in either RT or error scores.

3.4. High cognitive load

As can be seen in Fig. 2, the bargraph task again revealed a significant RVF advantage for both RTs [$F(1, 24) = 7.82, p < .01$] and errors [$F(1, 24) = 9.33, p < .01$], with faster and more accurate corrections to stimuli presented to the RVF (left hemisphere) (495 ms, 9.7% uncorrected initial erroneous responses) than to the LVF (right hemisphere) (536 ms, 23.3% uncorrected initial erroneous responses).

In the lexical decision task a significant LVF advantage was found for error scores [$F(1, 24) = 6.93, p < .05$]

with lower percentage of uncorrected initial erroneous responses to stimuli presented to the LVF (right hemisphere) ($M = 8.7$) than the RVF (left hemisphere) ($M = 22.1$). No trade off was found between RT and error scores. No other effects in the overall analysis reached statistical significance.

To eliminate the possibility that the superiority of the inferior hemisphere for corrections is due to longer initial responses, we calculated the correlation between RTs of erroneous initial responses and RTs of subsequent corrections. No correlation was found. To eliminate the possibility that the superiority of the inferior hemisphere for corrections is due to its “lower obligation” toward its initial processing, we subjected the number of false corrections (cases in which initial correct response is altered with an incorrect one) to a 3-way analysis of variance with the same design as above. No effect reached statistical significance.

4. Discussion

In the present experiment we looked for laterality patterns in error monitoring in both hemispheres. We found the classical asymmetries for initial responses in both right (bargraph judgment), and left (lexical decision) hemisphere tasks. Most importantly, we found a dramatic shift in these asymmetries for corrections: an

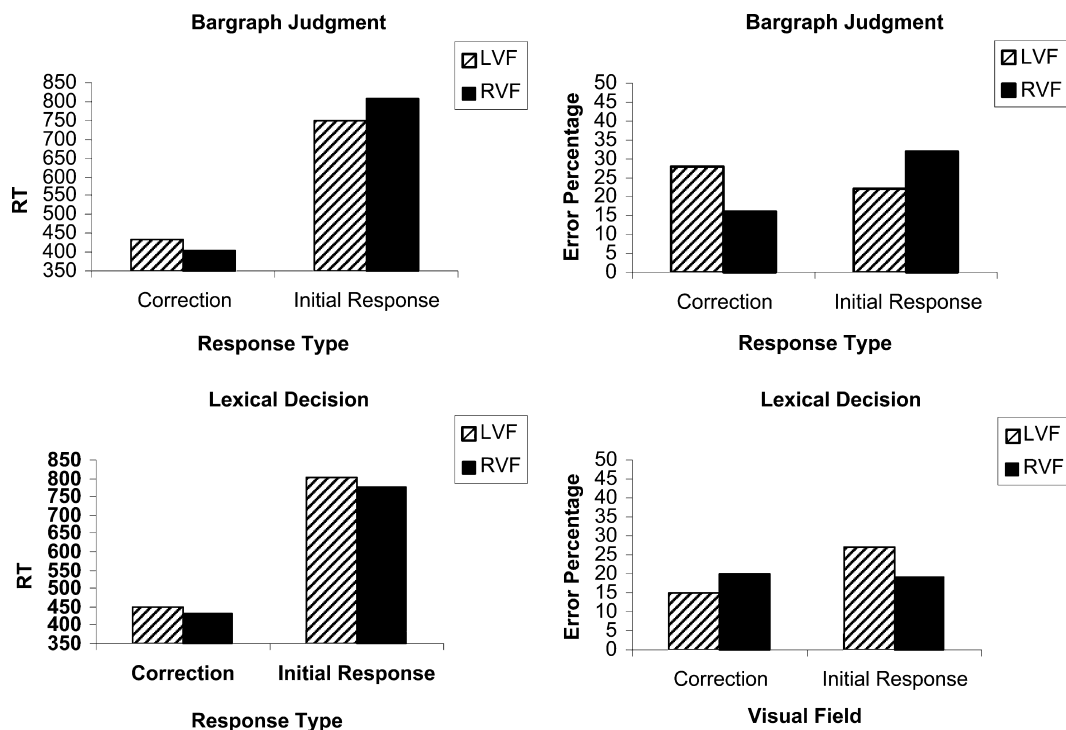


Fig. 1. Low cognitive load: RT and Error percentage as a function of VF and response type (notice that error percentage of initial responses is calculated as the percentage of incorrect responses out of total responses while error percentage of corrections is calculated as the percentage of uncorrected initial erroneous responses out of total erroneous responses).

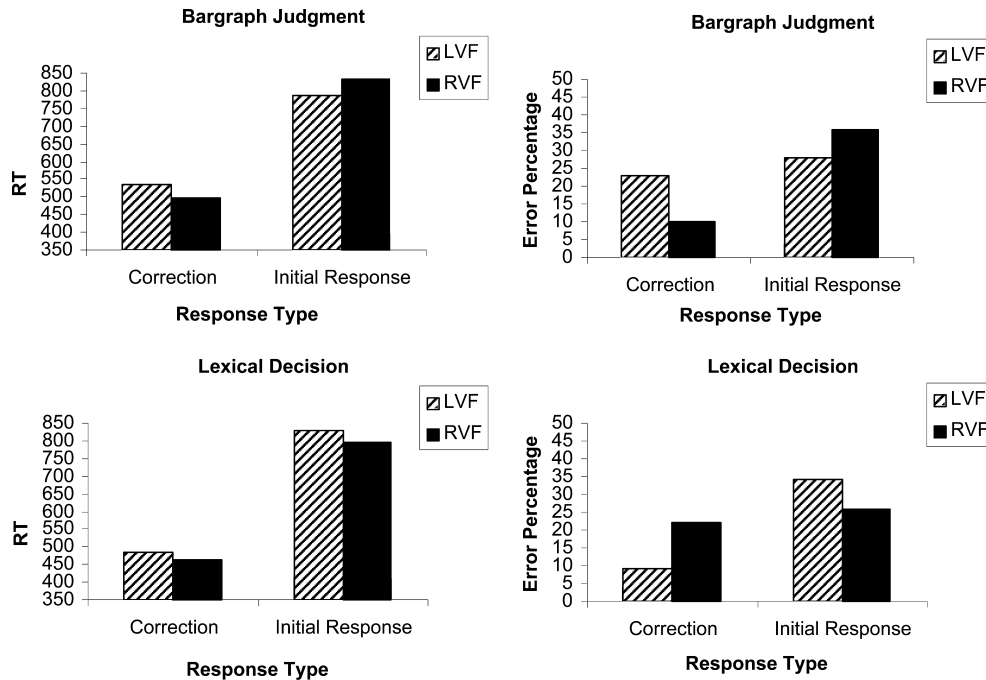


Fig. 2. High cognitive load: RT and Error percentage as a function of VF and response type (notice that error percentage of initial responses is calculated as the percentage of incorrect responses out of total responses while error percentage of corrections is calculated as the percentage of uncorrected initial erroneous responses out of total erroneous responses).

advantage for correction in the RVF for the bargraphs task at both load conditions, and an advantage for corrections in the LVF for the lexical decision task in the high load condition. The results support Zaidel's claim for a dissociation between initial processing and subsequent error monitoring. Moreover, past studies claimed that there is a RH advantage in either reaction to an external feedback about an error (Kaplan & Zaidel, 2001) or in compensation for errors (Iacoboni et al., 1997) in a lexical decision task. Our findings suggest that in spontaneous error detection the pattern of hemispheric monitoring is more complicated. Our design allowed us to compare error detection in a RH task to error detection in a LH task. We found that each hemisphere makes more efficient corrections in a task for which it is considered inferior. One possible explanation is that the inferior hemisphere always monitors its own errors better than the superior one does. This could be due to its "lower obligation" toward its initial process. However, if that is the case then the inferior hemisphere should also show more cases of false corrections (cases in which an initial correct response is replaced with an incorrect one), than the superior one. This was not found. Another possibility is that error monitoring begins before the initial response is executed. Hence, since it takes longer to the inferior hemisphere to do initial process and we measured correction RTs from the execution of the initial response, then, in the inferior hemisphere much of the error processing was done before RT measurement, resulting shorter correction RTs

in the inferior hemisphere than in the superior one. However, if that is the case than a correlation should be found between RTs of erroneous initial responses and RTs of subsequent corrections. No such correlation was found.

Zaidel (1987) suggested that each hemisphere monitors the ongoing process in the contralateral one. According to this explanation, in visual half field presentation paradigms, when a stimulus is presented to the VF of the inferior hemisphere, the superior one does the monitoring and vice versa. Thus, an advantage of presentation to the VF of the inferior hemisphere is always expected for corrections. Another issue which is of concern in this study is Zaidel's claim for labor division between the hemispheres in error monitoring because both initial response selection and its monitoring are resource demanding. In order to test this hypothesis we manipulated task load between subjects. Our findings suggest that when task becomes more demanding in terms of the load on working memory, the dissociation between initial processing and subsequent error monitoring grows. This is supported by the finding of no visual field advantage for corrections in the language task in the low cognitive load condition, but a LVF advantage was found for corrections in this task in the high load condition. One could argue that the difference between the cognitive load conditions stems from the difference in statistical power since more corrections were observed in the high load condition. However, in the low load condition no difference was found between

the LH task and the RH task in number of corrections. Nevertheless in the bargraphs task the number of corrections was sufficient to show the opposing VF effect from the initial responses. We suggest that the difference between the load conditions is qualitative, due to system overload, rather than quantitative, due to gaining more statistical power. We also suggest that the reason the bargraph judgement task showed reversed asymmetry for corrections at both load conditions while the lexical decision task showed reversed asymmetry for corrections only at the high load condition, is that reading is a well learned, automatic skill. Hence, in reading the cognitive system must be overloaded to dissociate initial decision from its monitoring, while in bargraph judgement since participants were not familiar with the task, the initial decision and its monitoring are dissociated even at low load conditions.

The hypothesis that each hemisphere monitors the ongoing processes in the other is rather appealing, however, the use of more direct means of measurement is needed to further establish this assumption. Although the poor spatial resolution of EEG does not allow for accurate hemispheric localization of the ERN, recent findings suggest that at least some kind of between-hemisphere cooperation is needed for error detection. Gehring and Knight (2000) recorded the ERN from patients with damage either to the left or to the right PFC and found that there was ERN activity on correct trials as well as on error trials. However, in controls, error trials generated greater ERN activity than correct trials. There is then an interaction between the left and the right PFCs that is necessary for error monitoring. Kaplan and Zaidel (2002) recently showed lack of spontaneous self-corrections in split brain patients. This can also be taken as evidence supporting the need for inter hemisphere interactions in monitoring for errors.

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