

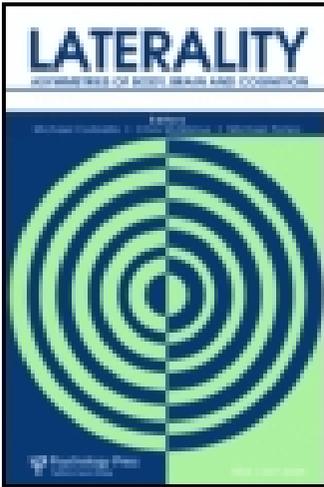
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### Different laterality patterns of the error-related negativity in corrected and uncorrected errors

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## Different laterality patterns of the error-related negativity in corrected and uncorrected errors

Eldad Yitzhak Hochman, Zohar Eviatar, Zvia Breznitz,  
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While measuring event-related brain potentials, a divided visual field paradigm was used to discern laterality patterns of the error-related negativity (ERN) in healthy human participants. Two tasks of hemispheric specialty were used (bargraph judgement, lexical decision) and a flanker task. For corrected errors in all tasks, stronger ERN amplitude was found following right visual field presentation. For corrected errors in the specialised tasks, shorter ERN latency was revealed on the side to which the stimulus was presented, while for uncorrected errors it was shorter on the other side. In the flanker task, ERN latency after corrected errors was shorter over the RH regardless of the side to which the stimulus was presented. Results are interpreted to reveal patterns of hemispheric specialisation, independence, and cooperation in error detection that depend on the type of error been committed.

**Keywords:** Error-related negativity; Cerebral hemispheres; Lateralisation.

The error-related negativity (ERN/NE) is a component of the event-related potential (ERP) considered to be associated with the execution of an incorrect response in serial choice reaction time tasks (e.g., Dehaene, Posner, & Tucker, 1994; Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Gehring, Goss, Coles, Meyer, & Donchin, 1993; Scheffers, Coles, Bernstein, Gehring, & Donchin, 1996). The ERN/NE starts at the onset of the electromyographic (EMG) activity preceding the overt error response and peaks about 50 to 100 ms thereafter (Gehring et al., 1993; Kopp, Rist, & Mattler, 1996). Because the ERN/NE is response related, it would be conceivable to assume that it would be affected by the side of the response. However, when the data from left-hand and right-hand responses were examined separately, the ERN/NE did not seem to be affected by the side of

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the response (Dehaene et al., 1994). This led Dehaene et al. (1994), to conclude that the error-processing system operates at an abstract level, independently of the exact motor effectors. Nevertheless, laterality patterns of the ERN/NE may appear at error-processing levels that are independent from the motor effectors. For instance, the mismatch theory of the ERN/NE holds that the ERN/NE is initiated after a comparator compares the representation of the actual response against a representation of the intended response (Coles, Scheffers, & Holroyd, 2001). It is possible that while stimulus processing occurs in one hemisphere, the comparison process takes place in the other hemisphere. Such laterality patterns may be revealed using the half visual field presentation paradigm (VHFP; see Bourne, 2006, for a review). VHFP asserts that initial processing occurs first, in the hemisphere that received the stimulus directly, without the need for callosal relay. Hence, fast responses are mostly affected by processes taking place in the receiving hemisphere. Because error processing occurs concurrently with the response, lateralising stimulus processing may lateralise the error process, allowing for the comparison of left hemisphere (LH) to right hemisphere (RH) error processing.

Although lateralisation of the ERN/NE had never been demonstrated, lateralisation of corrective behaviour was recently demonstrated at our lab, in a series of behavioural studies using VHFP. In the first study we compared tasks of LH superiority (lexical decision; Fernandino, Iacoboni, & Zaidel, 2007) to tasks of RH superiority (bargraph judgement; Boles, 1994), demonstrating an intrigue superiority of the inferior hemisphere for error correction (Hochman & Eviatar, 2004). In the second study we presented a stimulus aimed to interfere with error correction, either to the same side as the target or to the other side, and manipulated load of task (Hochman & Eviatar, 2006). In the high load condition, corrective behaviour was interfered more when interference was presented contralateral to the target. Based on these results we suggested that load of task may mediate the division of primary task performance and error processing across the hemispheres, thereby making error processing more efficient.

The goal of the present work was to examine lateralisation patterns of the response-monitoring process beyond error correction. Because the ERN/NE is observed at both corrected, and uncorrected errors (Falkenstein, Hohnsbein, & Hoormann, 1994, 1996; Fiehler, Ullsperger, & von Cramon, 2005; Gehring et al., 1993; Rodríguez-Fornells, Kurzbuch, & Münte, 2002), we assumed that studying laterality patterns of the ERN/NE in the two error types would shed some light on the contribution of the hemispheres to the development of an efficient error processing (i.e., an error process that ends up with error correction).

Laterality patterns of the ERN were explored using VHFP.<sup>1</sup> Participants were introduced to two tasks of hemispheric specialisation (lexical decision and bargraph judgement), and a task of no hemispheric specialisation (a shapes instead of letters version of the flanker task). In order to maximise the possibility of observing the same division of labour revealed in our behavioural studies, we induced task load in the same way as in our behavioural studies, by forcing the participants to update the stimulus–response mapping on each trial, prior and very close to target presentation. Our predictions were derived from our behavioural studies: by restricting initial processing to one hemisphere (using VHFP), an earlier ERN/NE peak is expected in the hemisphere that did not receive the stimulus. This effect may differ between corrected and uncorrected errors. A secondary aim of the current study was to address the question of hemispheric specialisation in response monitoring. If the classic hemispheric specialisation usually observed for correct responses also applies to response-monitoring mechanisms, both RT and accuracy of correct response and the amplitude of the ERN/NE are expected to show RVF (LH) advantage in the lexical decision task, and LVF (RH) advantage in the bargraph task, and no laterality patterns are expected in the flanker task.

## METHOD

### Participants

ERP data were gathered from 11 right-handed undergraduate University of Haifa students who had a mean age of 23 (5 male). All were healthy young

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<sup>1</sup> Following its assumed source in the anterior cingulate cortex (ACC; Dehaene et al., 1994; Gemba, Sasaki, & Brooks, 1986; Kiehl, Liddle, & Hopfinger, 2000), the ERN/NE is usually measured at frontomedial electrodes. Here, in order to define the latency of the ERN/NE within in each hemisphere, we measured the ERN/NE from frontolateral electrodes. Some results from modelling techniques such as BESA and LORETA suggest that the ERN/NE may be generated by resources more lateral than the ACC, thereby allowing for this unusual method of ERN/NE measurement. These studies suggested the supplementary motor area (SMA), and the pre-SMA as possible additional or sole generators of the ERN/NE (see Dehaene et al., 1994; Herrmann, Rommler, Ehliis, Heidrich, & Fallgatter, 2004; Luu, Tucker, Derryberry, Reed, & Poulsen, 2003). Other techniques also doubt the assumed sole ACC source of the ERN/NE. Intracranial ERP recordings suggest that sources at the medial frontal cortex, other than the caudal ACC may contribute to ERN/NE generation including the rostral ACC and the pre-SMA (Brazdil, Roman, Daniel, & Rektor, 2005; Brazdil et al., 2002). In another study that used transcranial magnetic stimulation (TMS) it was found that medial frontal stimulation of the pre-SMA led to an attenuation of the ERN/NE (Rollnik et al., 2004). If lateral generators contribute to ERN/NE initiation, laterality differences may be found by comparing ERN/NE epochs from both sides. Note, however, that the design of the current study is not aimed towards settling the ERN/NE generators debate, because laterality differences may occur as a direct result of lateral ACC activity.

adults, in good standing in their studies, with no known medical conditions involving the central nervous system.

## Materials and procedure

Each participant performed three tasks: lexical decision, bargraph judgement, and a flanker task. The order of tasks was changed and counter-balanced between participants.

*Bargraph task.* 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  $2.4 \times 6.7$  degrees of visual angle with the inner edge  $2^\circ$  from fixation. The centre of the bargraphs was level with the fixation point. Stimuli were presented for 90 ms. 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 right thumb.

*Lexical decision task.* The stimuli were two lists of 216 four-letter Hebrew words and 216 four-letter Hebrew pronounceable orthographically regular nonwords. The lists were mixed and randomised to create 432 trials. Letter strings were presented in black letters on a grey background for 130 ms. Letter strings were presented randomly either to the left of fixation or to the right of fixation, with the inner edge of each stimulus at  $1.5^\circ$  of visual angle from fixation. The participants were asked to indicate whether the letter string was a word or a nonword by pressing one of two keys (ascending or descending arrow) with their right thumb.

*Flanker task.* The task that was used to assess error monitoring is based on the original flanker task (Eriksen & Eriksen, 1974) that is often used in the error detection literature, with several modifications (Kaplan & Zaidel, 2002). The stimuli were black equilateral triangles, each side measuring  $0.75^\circ$  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 grey background, with their inner edge  $1.5^\circ$  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 it, both in the same visual field. The triangles were positioned so that their edges were  $1.5^\circ$  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. 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 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. Because compatible trials do not tend to produce errors, the number of trials was doubled compared to the two other tasks, to be 864 trials. The participants were instructed to respond to the central triangle.

### General procedure

The participants were seated with their head leaning against a back rest that held their eyes 57 cm from the screen. Prior to each task the participants performed a practice set of 80 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, using the thumb of the right hand. Instructions were to hold the thumb up between responses. Responses were made using a joystick. Participants were encouraged to spontaneously correct their erroneous responses by pressing the alternate key before the beginning of the upcoming trial. The sequence of events was the same in all of the experiments, with only the task changing among them. The sequence of events on each trial was as follows: The fixation stimulus was presented alone for 100 ms; it could be either a cross or a minus sign. When the fixation point was a cross, the stimulus–response mapping was as shown in Table 1.

When the fixation stimulus was a minus sign, the stimulus–response mapping was inverted—the inversion of the stimulus response mapping was used to increase load of task. (A similar manipulation had been used in our

TABLE 1  
Stimulus response mapping when the fixation is a plus sign

<i>Task</i>	<i>Stimulus–response mapping</i>	
	<i>Upper key</i>	<i>Lower key</i>
Lexical decision	Word	Nonword
Bargraphs	Odd number	Even number
Complex flankers	Arrow pointing down	Arrow pointing up

behavioural studies.) Inversions were pseudo-randomised to create an equal number of trials in both conditions. Immediately after the disappearance of the fixation stimulus, the target stimulus was presented. The next trial began 1000 ms after the first response to the target. Correction responses could be made until the beginning of the next trial.

## Psychophysiological recording

We recorded the electroencephalogram (EEG) from 32 scalp locations using tin electrodes (standard 10–20 system) referenced to the chin. The impedance of all electrodes did not exceed 5 k $\Omega$ . The vertical eye movements were recorded from electrodes placed below the left eye. EEG and EOG data were accumulated using a low-pass filter of 70 Hz and AD converted with 22-bit resolution. Sampling rate was 256 Hz. Eye movement correction procedure for each EEG trial was based on a linear regression method (Gratton, Coles, & Donchin, 1983). Response-locked ERPs were computed from artefact-free trials for each participant according to the different types of responses: incorrect-uncorrected responses, and incorrect-corrected responses, starting 100 ms before the response and continuing 600 ms post-response. Baseline used for response-locked averages was from  $-100$  to  $0$  ms. ERN/NE amplitude was defined as the largest negative pick in the  $-50$  to  $100$  ms interval post-response onset. ERN/NE latency was defined as the time interval between response onset and maximal amplitude. To gain statistical power, electrode sites were pooled to form three topographical regions. The following regions of interest (ROIs) were defined: left anterior (C3, C5, C1), medial anterior (Cz, Fz, AFz), right anterior (C4, C6, C2). Because the ERN/NE is usually defined on the medial line where it is most prominent, we first identified the ERN at medial electrodes. By this we ensured that our paradigm yielded a clear ERN/NE. We then defined the ERN/NE on lateral electrodes.

## RESULTS

Response times were defined as the time between target onset and button press. The data were evaluated statistically with repeated measures ANOVAs using Greenhouse-Geisser corrections for multiple comparisons when appropriate. In all tasks, inverted erroneous trials (erroneous trials in which stimulus–response mapping was inverted from the previous trial) and non-inverted erroneous trials (erroneous trials in which stimulus–response mapping was not inverted from the previous trial) were analysed together because no significant differences were found between these two types of trials for both RTs and percentage of corrected errors. In the flanker task

only incompatible trials were analysed because the compatible condition did not yield a sufficient number of errors to allow for a separate statistical analysis. A correction response was defined as a case of two button presses within a trial, with only the second button press being a correct one. To avoid reporting large amounts of statistical results not relevant to the issues under investigation, only relevant main effects or interactions are described.

## Behavioural data

*RT and accuracy analysis.* Reaction time and accuracy data are shown in Table 2. For RT, the three-way interaction of Task (three levels: flanker, lexical decision, and bar graph)  $\times$  Response Type (three levels: corrected, uncorrected erroneous responses, and correct responses),  $\times$  VF of stimuli (two levels: LVF, RVF), was significant,  $F(4, 40) = 32.44, p < .0001, \eta_p^2 = .47$ . As expected, correct responses reflected the classical performance asymmetries between the lateralised conditions: a LVF advantage in the bargraphs task indicating RH specialisation—RT,  $F(1, 10) = 13.65, p < .002, \eta_p^2 = .31$ —a RVF advantage in the lexical decision task indicating LH specialisation—RT,  $F(1, 10) = 41.10, p < .0001, \eta_p^2 = .32$ —and equivalence of VF performance in the flanker task, indicating no hemispheric specialisation for correct responses in this task. A significant main effect of Response Type was found,  $F(2, 10) = 56.77, p < .0001, \eta_p^2 = .37$ , indicating significantly longer RTs for uncorrected errors than for both corrected errors,  $F(1, 10) = 31.55, p < .0001, \eta_p^2 = .29$ , and correct responses,  $F(1, 10) = 26.87, p < .0001, \eta_p^2 = .34$ . Corrected errors were significantly shorter than correct responses,  $F(1, 10) = 27.45, p < .0001, \eta_p^2 = .45$ . These findings probably indicate that the corrected errors were anticipatory responses.

TABLE 2  
Response times and rates, tasks 1–3

Task	Corrected errors		Uncorrected errors		Correct responses	
	LVF	RVF	LVF	RVF	LVF	RVF
Bargraphs	563 (64.3)	585 (74.5)	737 (80.2)	747 (99.5)	695 (63.8)	726 (66.8)
	26 (9.4)	41 (14.5)	35 (13.5)	40 (17.6)	153 (33.3)	135 (29.4)
Lexical decision	595 (63.7)	573 (65.6)	761 (90.4)	728 (79.9)	723 (74.2)	696 (58.2)
	34 (10.7)	26 (8.2)	35 (8.6)	34 (12.1)	141 (36.1)	156 (45.2)
Flanker	498 (62.9)	516 (54.3)	631 (71.1)	585 (47.1)	501 (53.6)	519 (71.9)
	26 (10.1)	22 (8.2)	24 (5.9)	21 (7.3)	166 (28.4)	172 (37.2)

Mean response time (ms), and response rates for corrected errors, uncorrected errors, and correct responses broken down by VF; Tasks, 1–3.

Response times are depicted in the upper row and response rates are depicted in the lower row of each panel. Standard deviations are shown in parentheses.

A significant main effect was also found for Task,  $F(2, 10) = 41.02$ ,  $p < .0001$ ,  $\eta_p^2 = .33$ , indicating longer RTs for the bargraphs,  $F(1, 10) = 20.43$ ,  $p < .0001$ ,  $\eta_p^2 = .43$ , and the lexical decision,  $F(1, 10) = 23.75$ ,  $p < .0001$ ,  $\eta_p^2 = .39$ , than for the flanker task. This probably means that the flanker task was easier to perform than the specialised tasks. This conclusion is further supported by the accuracy analysis because a higher rate of correct responses was found in the flanker task than in both the lexical decision task,  $F(1, 10) = 34.17$ ,  $p < .0001$ ,  $\eta_p^2 = .36$ , and the bargraph task,  $F(1, 10) = 30.25$ ,  $p < .0001$ ,  $\eta_p^2 = .42$ . Finally, the classical performance asymmetries reported above for RT were also found for accuracy. A LVF advantage in the bargraphs task,  $F(1, 10) = 4.54$ ,  $p < .05$ ,  $\eta_p^2 = .46$ , a RVF advantage in the lexical decision task,  $F(1, 10) = 19.53$ ,  $p < .0005$ ,  $\eta_p^2 = .37$ , and equivalence of VF performance in the flanker task.

*Error corrections.* In a former behavioural study (Hochman & Eviatar, 2004), we demonstrated a superiority of the inferior over the superior hemisphere in correcting its own errors. In that study, proportion of corrected errors was calculated out of all errors. Here a similar analysis was conducted in order to examine whether this phenomenon was replicated. As shown in Table 2, the results from Hochman and Eviatar (2004) were replicated. For proportion of corrected errors out of all errors, a significant interaction of task  $\times$  VF was found,  $F(2, 20) = 4.66$ ,  $p < .01$ ,  $\eta_p^2 = .21$ . In the specialised tasks a higher proportion of corrected errors was found when stimuli were presented to the inferior hemisphere than when stimuli were presented to the superior hemisphere—bargraphs: LVF vs RVF,  $F(1, 10) = 7.17$ ,  $p < .002$ ,  $\eta_p^2 = .18$ ; lexical decision: LVF vs RVF,  $F(1, 10) = 5.32$ ,  $p < .04$ ,  $\eta_p^2 = .20$ . No significant effect of VF was found for the flanker task. To preclude the possibility that these effects were simply a result of difference in corrected errors RTs, we conducted a comparison within corrected errors between LVF and RVF in each of the specialised tasks. No significant differences were found.

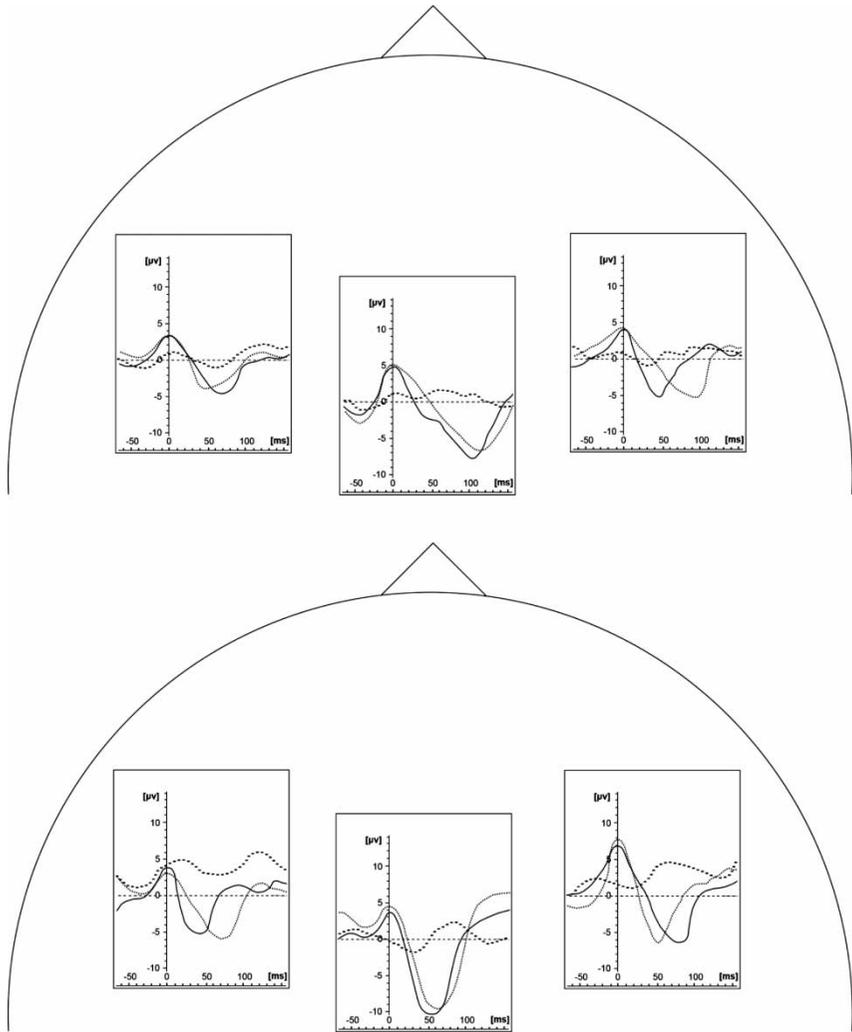
## ERP data

A four-way repeated-measures ANOVA with the within-participant factors Task (three levels: bargraph, lexical decision, and flanker task), Response Type (three levels: correct, corrected, and uncorrected erroneous responses), VF of stimuli (two levels: RVF and LVF), and Lateral Dimension of electrodes (three levels: right, middle, and left scalp region) was conducted on both the latency and the amplitude of the ERN/NE. Resulting interactions were analysed using lower-order ANOVAs.

*Amplitude.* The three-way interaction of Response Type  $\times$  VF  $\times$  Lateral Dimension was significant,  $F(4, 40) = 71.44, p < .0001, \eta_p^2 = .44$ . As shown in Figures 1, 2, and 3, in all tasks, within the corrected errors, the ERN/NE amplitude measured on the middle lateral dimension was stronger at RVF than at LVF—bargraphs: LVF,  $M = 8.1 \mu\text{V}$ , RVF,  $M = 10.3 \mu\text{V}$ ,  $F(1, 10) = 70.12, p < .0001, \eta_p^2 = .29$ ; lexical decision: LVF,  $M = 5.3 \mu\text{V}$ , RVF,  $M = 7.9 \mu\text{V}$ ,  $F(1, 10) = 46.42, p < .0001, \eta_p^2 = .36$ ; flanker: LVF,  $M = 4.9 \mu\text{V}$ , RVF,  $M = 9.9 \mu\text{V}$ ,  $F(1, 10) = 67.17, p < .0001, \eta_p^2 = .34$ . No other results reached statistical significance.

*Latency.* The four-way interaction of Task  $\times$  Response Type  $\times$  VF  $\times$  Lateral Dimension was significant,  $F(8, 80) = 72.87, p < .0001, \eta_p^2 = .15$ . As shown in Figures 1, 2, and 3, contradictory to our predictions, for corrected errors, in the specialised tasks the latency of the ERN/NE was shorter at the hemisphere to which the stimulus was presented. When stimuli were presented in the LVF, shorter latency was found at the RH than in the LH—bargraphs: LH,  $M = 68$  ms, RH,  $M = 49$ ,  $F(1, 10) = 42.11, p < .0001, \eta_p^2 = .11$ ; lexical decision: LH,  $M = 77$  ms, RH,  $M = 48$  ms,  $F(1, 10) = 12.85, p < .01, \eta_p^2 = .13$ . When stimuli were presented in the RVF, shorter latency was found at the LH than in the RH—bargraphs: LH,  $M = 46$  ms, RH,  $M = 86$  ms,  $F(1, 10) = 29.41, p < .0002, \eta_p^2 = .15$ ; Lexical decision, LH,  $M = 41$  ms, RH,  $M = 61$  ms,  $F(1, 10) = 34.77, p < .0004, \eta_p^2 = .09$ . In the flankers task, the latency was shorter at the RH regardless of VF—LVF: LH,  $M = 62$  ms, RH,  $M = 40$  ms,  $F(1, 10) = 22.16, p < .0006, \eta_p^2 = .08$ ; RVF: LH,  $M = 54$  ms, RH,  $M = 39$  ms,  $F(1, 10) = 7.78, p < .05, \eta_p^2 = .07$ .

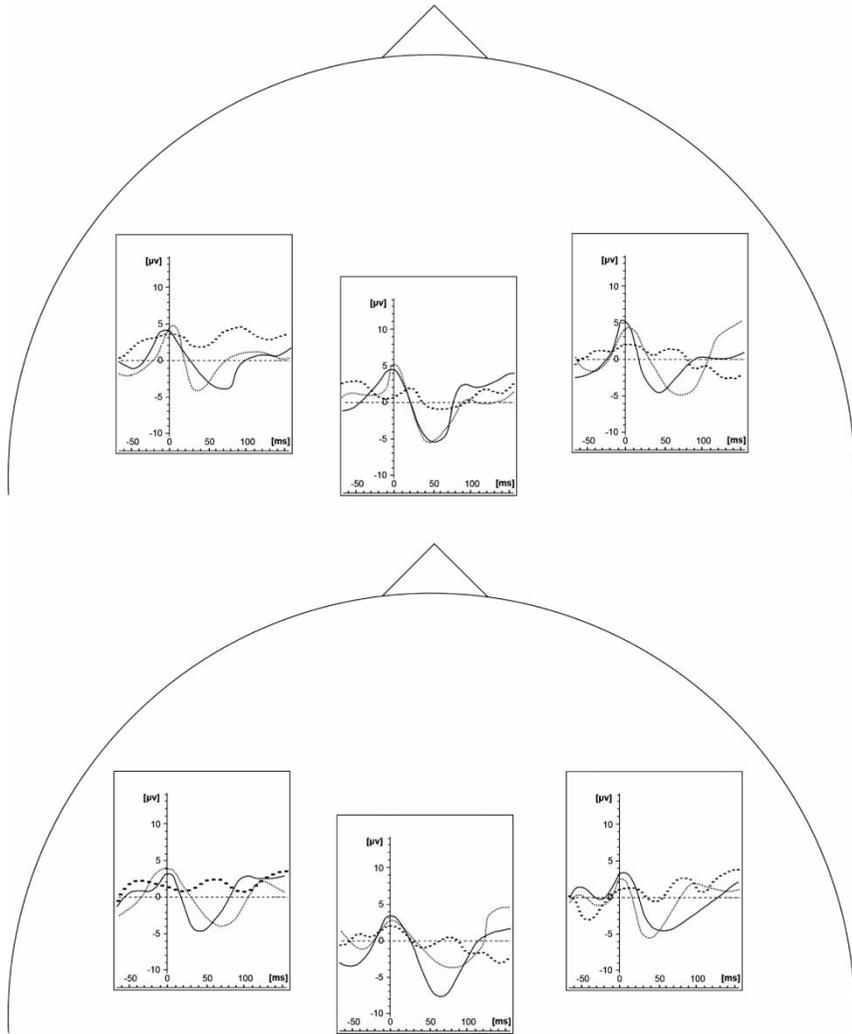
For uncorrected errors the results reversed. As shown in Figure 1, in the bargraph task, within the LVF shorter latency was found over the LH ( $M = 49$  ms) than over the RH ( $M = 97$  ms),  $F(1, 10) = 19.73, p < .002, \eta_p^2 = .24$ , while same comparison within the RVF revealed shorter latency over the RH ( $M = 51$  ms) than over the LH ( $M = 70$  ms),  $F(1, 10) = 10.31, p < .02, \eta_p^2 = .26$ . As shown in Figure 2, in the lexical decision task the results within the LVF revealed the same pattern as a comparison for uncorrected errors revealed shorter latency over the LH ( $M = 40$  ms) than over the RH ( $M = 72$  ms),  $F(1, 10) = 5.94, p < .06, \eta_p^2 = .21$ . The same comparison within the RVF revealed no significant difference; however the pattern was the same as in the bargraphs task, revealing shorter latency over the RH ( $M = 44$  ms) than over the LH ( $M = 70$  ms),  $F(1, 10) = 4.72, p < .08, ns, \eta_p^2 < .01$ . None of the effects reached statistical significance in the flanker task—LVF: LH,  $M = 67$  ms, RH,  $M = 55$  ms,  $F(1, 10) < 1, ns, \eta_p^2 < .01$ ; RVF: LH,  $M = 51$  ms, RH,  $M = 62$  ms,  $F(1, 10) < 1, ns, \eta_p^2 < .01$ ; results are depicted in Figure 3. No other results reached statistical significance.



**Figure 1.** Bargraph task: the ERN (grand average) in lateral and central ROIs. The upper skull shows the LRVF presentation and the lower skull shows the RRVF presentation. The solid line represents corrected errors, the dotted line represents uncorrected errors, and the dashed line represents correct responses.

## DISCUSSION

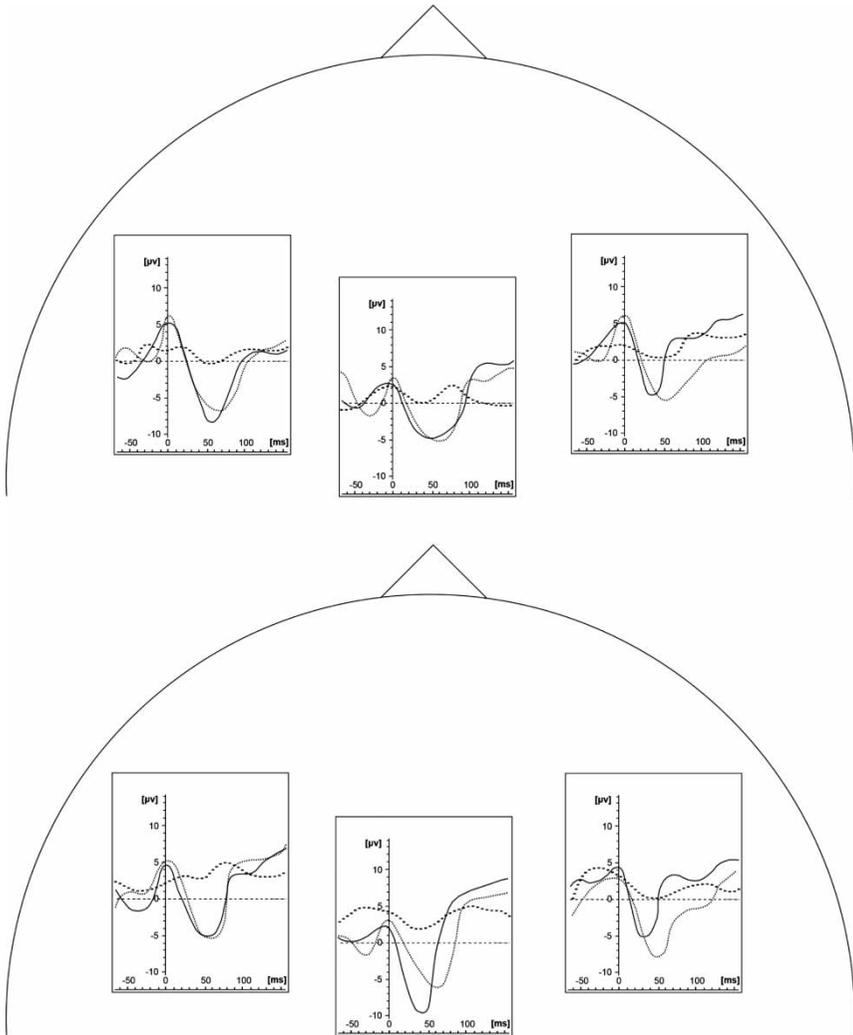
In the present study we used the divided visual field paradigm while recording evoked potentials in order to discern laterality patterns of the ERN/NE in corrected and uncorrected errors. The experimental questions



**Figure 2.** Lexical decision task: the ERN (grand average) in lateral and central ROIs. The upper skull shows the LVF presentation and the lower skull shows the RVF presentation. The solid line represents corrected errors, the dotted line represents uncorrected errors, and the dashed line represents correct responses.

were tested using two tasks for which divided visual field studies reveal performance asymmetries that are interpreted as reflecting hemispheric specialisation, and one task in which performance is equal in the two VFs.

The main objective of the current study was to discern possible characteristics of interhemispheric interactions in ERN/NE generation.



**Figure 3.** Flanker task: the ERN (grand average) in lateral and central ROIs. The upper skull shows the LVF presentation and the lower skull shows the RVF presentation. The solid line represents corrected errors, the dotted line represents uncorrected errors, and the dashed line represents correct responses.

The frontolateral ERN/NE measurements for corrected errors in the specialised tasks revealed shorter ERN/NE latency at the hemisphere contralateral to the VF of stimulus presentation (the receiving hemisphere). Both the mismatch theory (Coles et al., 2001) and the conflict detection theory (Yeung, Botvinic, & Cohen, 2004) of the ERN/NE argue that the

ERN/NE should peak at the exact point in time where either the efference copy of the actual response is established or the maximal response conflict is detected, in accordance. Hence, according to both models, shorter ERN/NE latency over the receiving hemisphere may indicate that either an efference copy had been established, or a maximal conflict had been detected at the receiving hemisphere, generating the ERN/NE independently of the other hemisphere. Zaidel, Clarke, and Suyenobu (1990) argued that each hemisphere functions as an independent cognitive unit complete with its own perceptual, motor, and linguistic abilities. The findings of the present study suggest that, at least for corrected errors in the specialised tasks, each hemisphere also has its own independent executive control, including the ability to detect errors.

However for uncorrected errors the results reversed, revealing a pattern of hemispheric interaction in error processing. For uncorrected errors, in the specialised tasks, ERN/NE latency was shorter at the non-receiving hemisphere—in the lexical decision at RVF (LH), this pattern was not significant. These results support the hypothesis (Hochman & Eviatar, 2006; Zaidel, 1987) that input processing and error processing are divided across the hemispheres.

The discrepancy between the laterality results for corrected and uncorrected errors may have resulted from the RT difference found between the two response types. While corrected errors were faster than correct responses, probably being anticipation errors resulting from impulsivity, uncorrected errors were longer than correct responses. A study by Scheffers and Coles (2000) showed longer RTs for errors than for correct responses under conditions of stimulus degradation. It is possible that presenting stimuli to half VF in the current study resulted in a stimulus degradation effect on uncorrected trials. The momentary difficulty in stimulus perception increased the attentional load at the receiving side, forcing the transfer of the error-monitoring process to the other side. This explanation is consistent with studies suggesting capacity limitations in error processing (Welford, 1959, 1980; see also Gehring & Fencsik, 2001; Hochman & Meiran, 2005; Laming, 1979), and with a recent study arguing for a load-dependent hemispheric division of labour, between primary task performance and the implementation of corrective behaviour (Hochman & Eviatar, 2006).

In the flanker task, for corrected errors, shorter ERN/NE latency was found over the RH, regardless of VF of stimulus presentation. It is not clear why the laterality patterns of the ERN in the flanker task are different from the specialised tasks. A possible explanation may be that in the flanker task most of the errors in the incongruent condition were caused by a distraction coming from the flanker. In this case, an error is detected when an

incongruency of the flanker and the target is perceived. Several studies have shown that the RH is specialised in its ability to attend to a larger portion of the VF as compared to the LH (Corbetta, Miezin, Shulman, & Petersen, 1993; Heilman & Van Den Abell, 1980; Proverbio, Zani, Gazzaniga, & Mangun, 1994). It is therefore possible that, on incongruent erroneous trials, the RH reacted to the incongruency faster than the LH regardless of whether information from the display was received directly or via callosal relay, hence the earlier generation of the error signal on the right side.

For corrected errors in all tasks, an advantage of RVF (LH) over LVF (RH) presentation was found for ERN/NE amplitude. These findings have two alternative explanations. First, because responses were always produced using the right hand, motor activity associated with the response was always located in the LH. This may have affected the ERN/NE. This explanation is in contrast with Dehaene et al. (1994), who failed to show effect of the motor operator on laterality patterns of the ERN/NE. These authors suggested that the error process operates independently of the exact motor contingencies. However our results propose otherwise, suggesting dependency between response monitoring and the exact response operator. Another possible explanation is the existence of LH specialisation for response monitoring. This explanation accords with a most recent study by Lutcke and Frahm (2008), which used high-resolution fMRI to show that the left part of the ACC is activated solely for error-related processes. The reason no effect was found for uncorrected errors may be related to the fact that in these responses the hemispheres may have had to interact in order to produce the ERN/NE as suggested in the previous paragraph in this section.

The RVF advantage found for ERN/NE generation in corrected errors for all tasks does not accord with the error correction results, which revealed a clear pattern of advantage of the VF of the inferior hemisphere in the specialised tasks: an RVF (LH) advantage in the bargraph task and LVF (RH) advantage in the lexical decision task (see also Hochman & Eviatar, 2004). The discrepancy between the electrophysiological results and the behavioural results can be resolved if we do not assume corrective behaviour to be a compensatory action, resulted directly from an error indication. A dissociation of the ERN/NE from corrective behaviour is also suggested by both patient data (Gehring & Knight, 2000; Ullsperger, 2006; Ullsperger & von Cramon, 2006a), and data acquired from healthy participants (Rodríguez-Fornells et al., 2002; Ullsperger & von Cramon, 2006b).

In summary, the results of the current study show patterns of hemispheric specialisation, independence, and integration in ERN/NE initiation, when

input is initially directed to one hemisphere. Laterality patterns varied as a function of task and whether the error was corrected or not. It is for future studies to further explore the role of these variables in the hemispheric division of labour between primary task performance and mechanisms of error processing.

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