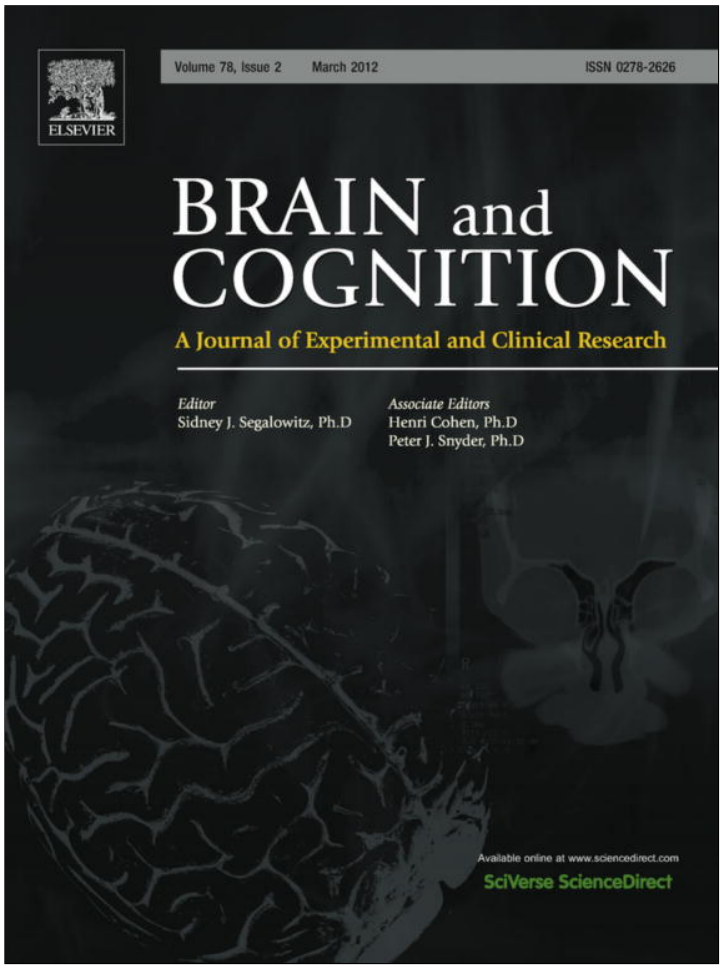

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Hemispheric asymmetries and cognitive flexibility: An ERP and sLORETA study

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ABSTRACT

Although functional cerebral asymmetries (FCAs) affect all cognitive domains, their modulation of the efficacy of specific executive functions is largely unexplored. In the present study, we used a lateralized version of the task switching paradigm to investigate the relevance of hemispheric asymmetries for cognitive control processes. Words were tachistoscopically presented in the left (LVF) and right visual half field (RVF). Participants had to categorise the words either based on their initial letters, or according to their word type. On half of the trials the task changed (switch trials) whereas on the other half it stayed the same (repeat trials). ERPs were recorded and the neural sources of the ERPs were reconstructed using standardised low resolution brain electromagnetic tomography (sLORETA). In the word type task, participants were faster on repeat trials when stimuli were presented in the RVF. In contrast, in the initial letter task participants were faster on repeat trials and in general more accurate after stimulus presentation in the LVF. In both tasks, no hemispheric asymmetries in reaction times were observed on switch trials. On the electrophysiological level, we observed a left lateralization of the N1 that was mediated by activation in the left extrastriate cortex as well as a greater positivity of the P3b after stimulus presentation in the RVF compared to the LVF that was mediated by activation in the superior parietal cortex. These results show that FCAs affect the neurophysiological correlates of executive functions related to task switching. The relation of neurophysiological and behavioural asymmetries is mediated by task complexity, with more complex tasks leading to more interhemispheric interaction and smaller left–right differences in behavioural measures. These findings reveal that FCAs are an important modulator of executive functions related to cognitive flexibility.

1. Introduction

Cognitive control processes mediated via basal ganglia-prefrontal loops play a major role in the organisation of human behaviour and include mechanisms related to inhibition (Sehlmeyer et al., 2010), selection (Beste, Saft, Andrich, Gold, & Falkenstein, 2008) and correction of erroneous actions (Beste, Willemssen, Saft, & Falkenstein, 2009). A key aspect of cognitive control is cognitive flexibility, the ability to swiftly switch between different tasks. One of the major experimental paradigms to investigate this aspect of executive functions is the task switching paradigm (Allport, Styles, & Hsieh, 1994; Karayanidis, Coltheart, Michie, & Murphy, 2003; Kiesel et al., 2010; Monsell, 2003). In cued task-switching experiments, a cue at the beginning of each trial indicates which task out of a set of two or more the participant has to perform in this trial. On so-called switch trials the task that has to be performed changes compared to the trial before, whereas on repeat trials it does not. Typically, participants react slower on switch than on repeat trials, a phenomenon called switch costs (Jamadar, Hughes, Fulham, Michie, & Karayanidis, 2010; Rogers & Monsell, 1995; Wylie & Allport, 2000).

Performance in paradigms that assess executive functions is influenced by information processing in the bottom-up channel (e.g. Knudsen, 2007). However, depending on the type of stimuli used, one hemisphere is more efficient in processing than the other. For example, the left hemisphere is more efficient in processing verbal stimuli than the right hemisphere (Corballis, 2009; Hugdahl, 2005). It has been shown that these so-called functional cerebral asymmetries (FCAs) modulate the efficacy of executive functions related to response inhibition processes, with initial stimulus presentation in the non-dominant hemisphere leading to a less efficient inhibition process (Measso & Zaidel, 1990; Ocklenburg, Güntürkün, & Beste, 2011). Although likely, it is not clear whether FCA's also modulate executive functions involved in task switching. Even more important is the question of which neurophysiological processes are involved and in what brain areas this modulation takes place. This information is necessary to achieve a more comprehensive mechanistic explanation of the neural events subserving task switching. To this end, we use a cued task switch paradigm with tachistoscopic presentation of verbal stimuli in the left (LVF) or right visual field (RVF).

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Participants had to categorise the words either based on their initial letters, or according to their word type. The simpler initial letter task can be solved by relying on a perceptual analysis of spatial features of the two initial letters, a cognitive process that is mediated by the right hemisphere (Vogel, Bowers, & Vogel, 2003). The more complex name identity task, however, can only be solved by using a verbal information processing strategy that is mediated by the left hemisphere (Corballis, 2009; Hugdahl, 2005). Therefore, we would expect participants to be more accurate and faster on RVF compared to LVF trials when performing the word type task, but more accurate and faster on LVF compared to RVF trials when performing the initial letter task. These hemispheric asymmetries should be reduced on switch compared to repeat trials, since switch trials are more complex than repeat trials as they include additional cognitive processes including prospective reconfiguration processes, active control processes, as well as passive task interference processes (Rushworth, Passingham, & Nobre, 2005). This increasing task complexity has been linked to reduced hemispheric asymmetries (Hausmann, Kirk, & Corballis, 2004) as well as greater interhemispheric interaction in order to solve a task (Banich & Belger, 1990; Bayer, Kessler, Güntürkün, & Hausmann, 2008; Weissman & Banich, 2000; Welcome & Chiarello, 2008). Moreover, we expect participants to be faster and more accurate on repeat- compared to switch-trials.

On the neurophysiological level, FCAs should be evident in two different cognitive processing stages when examined using event-related potentials (ERPs): On the one hand, FCAs for processing of verbal stimuli have an effect on stimulus-driven attentional processing as reflected by a left-lateralization of the N1 ERP-components. The N1 is a negative ERP component that is supposed to reflect mechanisms that orient attention towards visual stimuli (Beste, Baune, Falkenstein, & Konrad, 2010; Beste et al., 2008; Herrmann & Knight, 2001; Hillyard & Anllo-Vento, 1998; Wascher & Beste, 2010) or mechanisms involved in the categorisation of these stimuli (Grossi, Savill, Thomas, & Thierry, 2010). The N1 is the earliest ERP component that reflects recognition of verbal stimuli (Spironelli & Angrilli, 2009) and the greater efficacy of the left hemisphere in processing of verbal stimuli is reflected by a left-lateralized N1 (Grossi et al., 2010; Proverbio, Cok, & Zani, 2002; Spironelli & Angrilli, 2007). Consequently, brain areas that have been linked to the N1 like the extrastriate cortex, dorsal occipito-parietal and ventral occipito-temporal areas (Gomez-Gonzalez, Clark, Fan, Luck, & Hillyard, 1994; Herrmann & Knight, 2001; Yamazaki et al., 2000) should show FCA-dependent activation differences.

In addition to the early stimulus-driven attentional processes reflected by the N1, FCAs have also been shown to modulate later ERP components (Ocklenburg et al., 2011). In this regard the P3b is important for task switching performance (Gajewski et al., 2010; Hsieh, 2006; Kok, 2001). The P3b has been suggested to reflect a memory guided stimulus evaluation process (Kok, 2001). One of the main theoretical accounts of P3b function is the context-updating or schema revision approach (Donchin, 1981; Polich, 2007). This processing capacity approach suggests that a stimulus entering the processing system elicits a memory comparison process which checks whether the current stimulus is identical to the previous stimulus or not. Should the incoming stimulus be different compared to the trial before, the subject has to allocate additional attentional resources to this stimulus and the neural representation of the stimulus environment is updated. This process leads to a more pronounced P3b potential (Polich, 2007). In accordance with this approach of P3b function, a greater positivity of the P3b following a switch cue compared to a cue that indicates a repeat was observed in cued task-switching experiments (Barcelo, Escera, Corral, & Periáñez, 2006; Jost, Mayr, & Rösler, 2008; Nicholson, Karayanidis, Davies, & Michie, 2006; Nicholson, Karayanidis, Poboka, Heathcote, & Michie, 2005, but see Rushworth et al., 2005). According to the suggestion that the P3b is reduced when a task is more demanding (Polich, 2007), we expect a smaller P3b amplitude after stimulus presentation in the LVF, since the right hemisphere is non-dominant for the processing of verbal information.

2. Methods

2.1. Subjects

A total of 25 adult volunteers (10 male and 15 female) with no history of any neurological or psychiatric diseases participated in the present study. The mean age of participants was 25.32 years (range 21–38 years) and all of them were right-handed (mean laterality quotient 96.91; range 80–100), as assessed with the Edinburgh handedness inventory (Oldfield, 1971). All participants received a reimbursement of 20€ for their participation, gave written informed consent and were treated in accordance with the declaration of Helsinki. The study was approved by the ethics committee of the faculty of psychology of the Ruhr-University of Bochum.

2.2. Experimental paradigm

At the beginning of the experiment, participants were instructed to place their head on a chin rest placed at a distance of 57 cm from the screen and to fixate on a black fixation cross that was presented in the middle of the screen throughout the experiment. Stimuli consisted of eight German five-letter words in upper case letter (HUMOR, HAFEN, HOLEN, HEBEN, MUSIK, MORAL, MALEN, MIXEN; English translation: humor, harbour, to fetch, to lift, music, morale, to paint, to mix) that were presented tachistoscopically on a 17 inch CRT computer monitor with a refresh rate of 80 Hz either in participants left visual field (LVF) or right visual field (RVF). The stimuli had a font size of 10 and their inner edge was located 2° of visual angle away from the central fixation cross. At the beginning of each trial, the central fixation cross was exchanged for a coloured square with a height and width of 0.4° visual angle. A red square was used as cue to announce an initial letter task (participants had to indicate whether the word began with H or M), whereas a green circle was used as cue to announce a word type task (participants had to indicate whether the word was a noun or a verb). Responses consisted of pressing one out of two vertically arranged keys on a custom-made response pad. Throughout the experiment, one key had to be pressed with the left and the other with the right index finger. This stimulus–response assignment was counterbalanced across participants. Each trial consisted of the tachistoscopic presentation of the cue and the stimulus for 185 ms and a subsequent presentation of the central fixation cross. The simultaneous presentation of cue and target was chosen since it has been shown that priming effects can decrease laterality effects for language processing (Saetrevik & Hugdahl, 2007). Participants had to react within this 2185 ms time before the next trial began. During the inter-trial interval (randomized between 900 and 1300 ms) only the central fixation cross was presented. Overall, the experiment consisted of 50 practise trials that were excluded from later analysis and 960 experimental trials (240 switch and 240 repeat trials for each task). The two tasks were presented in randomized order, as were switch and repeat trials. In half of the trials stimuli were presented in the left visual field (LVF), in the other half in the right visual field (RVF) in randomized order.

2.3. EEG recording and analysis

EEG was recorded from 65 Ag–AgCl electrodes and standard scalp positions (FCz, FP1, FP2, F7, F3, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, TP9, CP5, CP1, CP2, CP6, TP10, P7, P3, Pz, P4, P8, PO9, O1, Oz, O2, PO10, AF7, AF3, AF4, AF8, F5, F1, F2, F6, FT9, FT7, FC3, FC4, FT8, FT10, C5, C1, C2, C6, TP7, CP3, CPz, CP4, TP8, P5, P1, P2, P6, PO7, PO3, POz, PO4, PO8) against a reference electrode located at Cz with a sampling rate of 500 samples per second. Electrodes were placed according to the extended 10–20 system using an elastic cap that was positioned relative to nasion, inion and the left and right tragus. All electrode impedances were maintained below 5 kΩ and a band-pass filter ranging from 0.5 to 20 Hz (48db/oct) was applied to the data. After filtering, the raw data were visually inspected. All trials containing rarely occurring technical artefacts (e.g. due to head movements) were removed from further analysis. Overall, the amount of trials rejected by this procedure was below 5% of all trials in each condition and each EEG-channel. To correct for periodically recurring artefacts (pulse artefacts, as well as horizontal and vertical eye movements) an independent component analysis (ICA) was then applied to the unepoched data set. Afterwards, the EEG data were epoched and automated artefact rejection procedures were applied to ensure that no non-physiological artefacts were included in the ERP data. Rejection criteria included a maximum voltage step of more than 50 μV/ms, a maximal value difference of 200 μV in a 200 ms interval or activity below 0.1 μV. Then the data were CSD-transformed (current source density transformation; Perrin, Pernier, Bertrand, & Echallier, 1989) in order to eliminate the reference potential from the data. After the CSD-transformation, data were corrected relative to a baseline extending from 200 ms before stimulus presentation until stimulus onset. Data on trials with correct behavioural responses were analysed stimulus-locked, with stimulus onset set as time point zero. Analysis epochs had a length of 1200 ms (ranging from 200 ms before stimulus onset to 1000 ms after stimulus onset). N1 amplitudes were evaluated relative to the peak of the preceding P1 component and P3b amplitudes were evaluated relative to baseline. The electrodes used for quantification were determined based on the scalp topography of the components (see Section 3). On the basis of the topographies the N1 amplitudes were quantified at electrodes PO7 and PO8 whereas P3b potentials were quantified at electrodes Pz, P1 and P2.

2.4. sLORETA analysis

Source localisation was conducted for ERP-components that differed between left and right hemispheric stimulation using sLORETA (standardised low resolution brain electromagnetic tomography; Pascual-Marqui, 2002), a newer version of LORETA (low resolution brain electromagnetic tomography; Pascual-Marqui, Michel, & Lehmann, 1994; Pascual-Marqui et al., 1999). Basically, sLORETA gives a single linear solution to the inverse problem of localisation of brain function based on extracranial measurements (Marco-Pallares, Grau, & Ruffini, 2005) and produces images of standardised current density with no localisation bias (Pascual-Marqui, 2002; Sekihara, Sahani, & Nagarajan, 2005). The localisation accuracy of sLORETA has been validated in simultaneous EEG/fMRI studies (Mulert et al., 2004; Olbrich et al., 2009; Vitacco, Brandeis, Pascual-Marqui, & Martin, 2002). For sLORETA the intracerebral volume is partitioned in 6239 voxels at 5 mm spatial resolution and the standardised current density at each voxel is then calculated in a realistic head model (Fuchs, Kastner, Wagner, Hawes, & Ebersole, 2002) using the MNI152 template (Mazziotta et al., 2001). In the present study the voxel-based sLORETA-images were compared between stimulus presentation in the LVF and RVF using the sLORETA-built-in voxel-wise randomisation tests with 5000 permutations, based on statistical non-parametric mapping (Holmes, Blair, Watson, & Ford, 1996). Voxels with significant differences ($p < .01$, corrected for multiple comparisons) between LVF and RVF presentation were located in the MNI-brain and Brodmann areas (BAs) as well as coordinates in the MNI-brain were determined using the software (www.unizh.ch/keyinst/NewLORETA/sLORETA/sLORETA.htm).

2.5. Statistics

The behavioural data (reaction times and error rates) were analysed using repeated-measures analyses of variance (ANOVAs) with the within-subjects task (initial letter task, word type task), trial type (switch trial, repeat trial) and visual half-field (RVF, LVF).

The electrophysiological data (i.e. amplitudes and latencies) were analysed using ANOVAs with the within-subjects factors electrode (N1: PO7 & PO8; P3b: Pz, P1 & P2), task (initial letter task, word type task), trial type (switch trial, repeat trial) and visual half-field (RVF, LVF). All p-levels for post hoc t-tests were adjusted using Bonferroni correction. Effect sizes were given as the proportion of variance accounted for (partial η^2). As a measure of variability, the standard error of the mean (SE) together with the mean values are given. All statistical analyses were computed by using the software package PASW 18.0.

3. Results

3.1. Behavioural data

3.1.1. Reaction times and error rates

Median reaction times and error rates for repeat and switch trials for both tasks are shown in Fig. 1.

Participants were faster in the word type task (885 ms ±30) than in the initial letter task (946 ms ±35) as indicated by a significant main effect task ($F_{(1,24)} = 21.20$; $p < 0.001$; $\eta^2 = 0.47$). In addition, a significant main effect trial type ($F_{(1,24)} = 76.92$; $p < 0.001$; $\eta^2 = 0.76$) revealed that participants were faster on repeat (848 ms ±29) than on switch trial (983 ms ±36). The significant interaction task × visual field ($F_{(1,24)} = 14.70$; $p < 0.001$; $\eta^2 = 0.38$) indicated that in the word type task, participants were faster after stimulus presentation in the RVF (874 ms ±31) compared to the LVF (897 ms ±30; post hoc test: $p < 0.05$), while no significant differences were observed in the initial letter task (LVF: 941 ms ±34; RVF: 951 ms ±36; post hoc test: $p = 0.27$). This interaction was, however, modulated by trial type, as indicated by the two significant interactions task × trial type ($F_{(1,24)} = 42.39$; $p < 0.001$; $\eta^2 = 0.64$) and task × trial type × visual field ($F_{(1,24)} = 19.23$; $p < 0.001$; $\eta^2 = 0.45$). In both tasks, no visual half-field dependent differences were observed on switch trials (initial letter task: LVF: 1045 ms ± 40; RVF: 1031 ms ± 39; post hoc test: $p = 0.46$; word type task: LVF: 931 ms ± 33; RVF: 926 ms ± 36; post hoc test: $p = 1.00$). On repeat trials, however, visual half-field dependent differences in reaction times were observed. In the word type task, participants were faster after stimulus presentation in the RVF (821 ms ± 27) compared to the LVF (863 ms ± 29; post hoc test: $p < 0.01$). This pattern was reversed in the initial letter task (LVF: 837 ms ± 30; RVF: 871 ms ± 35; post hoc test $p < 0.05$). All other main effects and interactions failed to reach significance (all F's < 0.85; all p's > 0.36).

To further investigate the three-way interaction, two separate follow-up ANOVAs with the within-subjects task (initial letter task, word type task) and visual half-field (RVF, LVF) were calculated for the two trial types. While the interaction task × visual field failed to reach significance when only switch trials were analysed ($F_{(1,24)} = 0.51$; $p = 0.49$), it was significant when only repeat trials

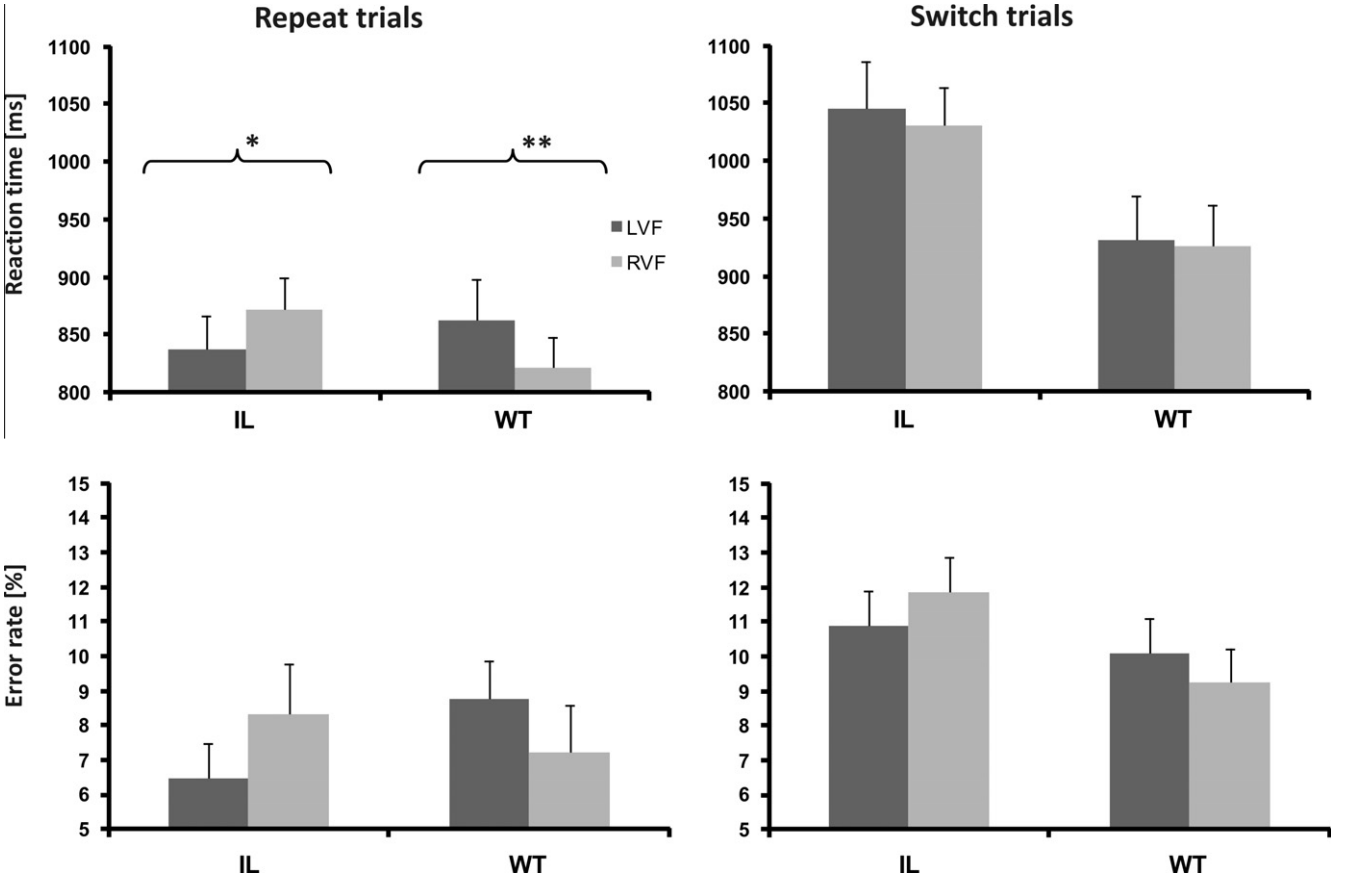

Fig. 1. Median reaction times and error rates for repeat (left) and switch trials (right) in the initial letter task and the word type task. Dark grey bars show LVF trials and light grey bars show RVF trials. Significant post hoc comparisons are indicated by asterisks, with * = $p < 0.05$ and ** = $p < 0.01$.

were analysed ($F_{(1,24)} = 38.47$; $p < 0.001$; $\eta^2 = 0.62$). While participants were faster after stimulus presentation in the RVF (821 ms ± 27) compared to the LVF (863 ms ± 29; post hoc test: $p < 0.001$) when conducting the word type task, they were faster after stimulus presentation in the LVF (837 ms ± 30) compared to the RVF (871 ms ± 35; post hoc test: $p < 0.01$) when conducting the initial letter task.

Participants made less errors on repeat (7.69% ± 0.98) than on switch trials (10.53% ± 1.15) as revealed by a main effect trial type ($F_{(1,24)} = 31.74$; $p < 0.001$; $\eta^2 = 0.57$). An interaction task × trial type ($F_{(1,24)} = 5.74$; $p < 0.05$; $\eta^2 = 0.19$), indicated that the difference between switch and repeat trials was more pronounced in the initial letter task (switch trials: 11.38% ±1.33; repeat trials: 7.38% ±0.95; difference: 4%; post hoc test: $p < 0.001$) then in the word type task (switch trials: 9.67% ±1.35; repeat trials: 8.00% ±1.24; difference: 1.67%; post hoc test: $p < 0.05$). Moreover, there was a significant interaction task × visual half-field ($F_{(1,24)} = 4.87$; $p < 0.05$; $\eta^2 = 0.17$) indicating that in the initial letter task, participants made less errors after stimulus presentation in the LVF (8.68% ±1.06) compared to stimulus presentation in the RVF (10.08% ±1.21; post hoc test: $p < 0.05$), whereas in the word type task no significant difference between stimulus presentation in the LVF (9.43% ±1.45) compared to stimulus presentation in the RVF (8.23% ±1.33) was observed (post hoc test: $p = 0.32$). All other main effects and interactions failed to reach significance (all F's < 1.54; all p's > 0.23).

In order to investigate the relationship between reaction times and error rates, Pearson correlation coefficients were calculated for all conditions (see Table 1). For the initial letter task, significant correlations between reaction times and error rates were found for LVF repeat trials ($r = 0.48$; $p < 0.05$). For the word type task, significant correlations were also found for LVF repeat trials ($r = 0.45$; $p < 0.05$) and additionally for both RVF repeat ($r = 0.56$; $p < 0.01$) and RVF switch trials ($r = 0.48$; $p < 0.05$). Since all of these correlations were positive, no speed-accuracy trade-off took place in the present experiment. Instead, participants who made more errors also had longer reaction times.

Table 1
Pearson correlation coefficients between error rates and reaction times for switch and repeat trials with stimulus presentation in the left (LVF) or right visual field (RVF) in the initial letter and the word type task.

	Initial letter task	Word type task
LVF repeat	0.48*	0.45*
LVF switch	0.19	0.26
RVF repeat	0.36	0.56**
RVF switch	0.24	0.48*

* $p < 0.05$.
** $p < 0.01$.

3.1.2. Neurophysiological data

ERPs on switch- and repeat-trials for stimulus presentation in the LVF and RVF are shown in Fig. 2.

3.1.3. N1

Based on the topography of the N1, the electrodes PO7 (left hemisphere) and PO8 (right hemisphere) were chosen for data analysis (see Fig. 2). For the amplitudes the ANOVA revealed a significant main effect of electrode ($F_{(1,24)} = 4.95$; $p < 0.05$; $\eta^2 = 0.17$),

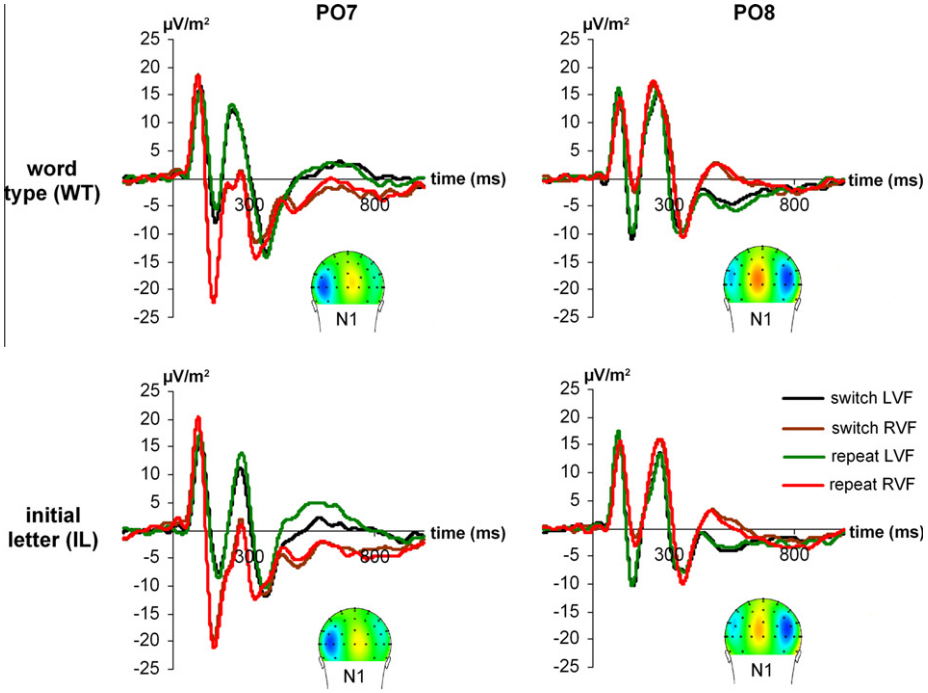

Fig. 2. Stimulus-locked ERP components at electrodes PO7 and PO8 in the word type and initial letter task for switch and repeat trials after stimulus presentation in the LVF and RVF. Representative topographical maps for the N1 on repeat trials after stimulus presentation in the contralateral visual field are given. All topographies were generated from the peak of the N1 and determined relative to baseline. Time point 0 denotes the point of stimulus presentation.

indicating that the amplitude of the N1 was more negative at electrode PO7 (−46.16 ± 7.16) than at electrode PO8 (−35.19 ± 4.54). Moreover a main effect of visual half-field occurred ($F_{(1,24)} = 5.38$; $p < 0.05$; $\eta^2 = 0.18$), indicating that the amplitude of the N1 was more negative after stimulus presentation in the RVF (−42.83 ± 5.99) than after stimulus presentation in the LVF (−38.52 ± 5.05). Furthermore, an interaction electrode × visual half-field ($F_{(1,24)} = 13.35$; $p < 0.001$; $\eta^2 = 0.36$) emerged, indicating that at electrode PO7 the amplitude of the N1 was more negative after stimulus presentation in the RVF(−53.09 ± 8.17) compared to the LVF (−39.23 ± 6.50; post hoc test: $p < 0.01$), whereas at electrode PO8 a trend towards the opposite pattern was observed (LVF: −37.80 ± 4.97; RVF: −32.57 ± 4.49; post hoc test: $p = 0.07$). Moreover, an interaction electrode × task × trial type ($F_{(1,24)} = 7.65$; $p < 0.05$; $\eta^2 = 0.24$) emerged. All other main effects and interactions failed to reach significance (all F's < 3.96; all p's > 0.06).

3.1.4. P3b

Based on the topography of the P3b, the electrodes Pz, P1 (left hemisphere) and P2 (right hemisphere) were chosen for data analysis (see Fig. 3).

For the amplitudes, the ANOVA revealed a significant main effect of electrode ($F_{(2,48)} = 4.55$; $p < 0.05$; $\eta^2 = 0.16$), indicating that the P3b was more positive at Pz (26.87 ± 3.23) than at P1 (22.91 ± 2.65) and P2 (22.84 ± 2.94). Moreover, the P3b was more positive after stimulus presentation in the RVF (26.89 ± 3.13) compared to the LVF (21.52 ± 2.61) as indicated by a main effect of visual half-field ($F_{(1,24)} = 19.05$; $p < 0.001$; $\eta^2 = 0.45$). In addition, a significant main effect of trial type ($F_{(1,24)} = 8.38$; $p < 0.01$; $\eta^2 = 0.26$) was observed, with the P3b being more positive on switch (24.67 ± 2.81) compared to repeat (23.74 ± 2.84) trials. This effect reached significance only in the initial letter (switch trials: 25.53 ± 2.89; repeat trials: 23.50 ± 2.86; post hoc test: $p < 0.001$) but not in the word type (switch trials: 23.80 ± 2.75; repeat trials: 23.99 ± 2.84; post hoc test: $p = 0.69$) task (interaction task × trial type; $F_{(1,24)} = 10.93$; $p < 0.01$; $\eta^2 = 0.31$). All other main effects

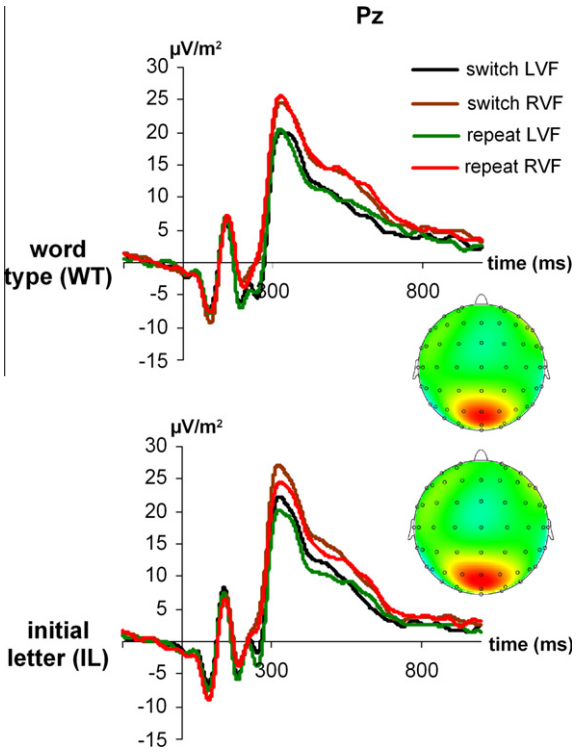

Fig. 3. Stimulus-locked ERP components at electrode Pz in the word type and initial letter task for switch and repeat trials after stimulus presentation in the LVF and RVF. Representative topographical maps for the P3b on repeat trials after stimulus presentation in the right visual field for the word type (upper map) and initial letter task (lower map) are given. All topographies were generated from the peak of the P3b and were determined relative to baseline. Time point 0 denotes the point of stimulus presentation.

and interactions failed to reach significance (all F's < 2.94; all p's > 0.08).

3.1.5. sLORETA analysis

The results of the sLORETA analysis are given in Fig. 4.

3.1.6. N1

As can be seen in Fig. 4 the difference in N1 amplitudes between presenting stimuli in the LVF and RVF was due to differences in activation in the left extrastriate cortex. Activation differences were observed in left BA18 (centre of activation: coordinates in the MNI-brain −31, −24, −2) for both tasks and left BA19 (centre of activation: coordinates in the MNI-brain −54, −66, −9) for the initial letter task, only. Stimulus presentation in the LVF produced less activation than presentation in the RVF.

3.1.7. P3b

As can be seen in Fig. 3 the difference in P3b amplitudes between presenting stimuli in the LVF and RVF was due to bilateral differences in activation in the superior parietal cortex (BA7; centre of activation: coordinates in the MNI-brain 24, −66, 57) in both tasks. Slightly stronger activation differences were observed in the right hemisphere. Stimulus presentation in the LVF produced less activation than presentation in the RVF.

4. Discussion

The aim of the present study was to investigate the modulation of executive processes involved in task switching by functional cerebral asymmetries (FCAs). As expected, participants were faster and more accurate on repeat trials than on switch trials, reflecting the well known switch costs in task-switching paradigms (Jamadar et al., 2010; Rogers & Monsell, 1995; Wylie & Allport, 2000). On repeat trials in the word type task, participants were faster after stimulus presentation in the RVF, reflecting the greater efficacy of the left hemisphere in verbal information processing (Corballis, 2009; Hugdahl, 2005). In contrast, in the initial letter task participants were faster on repeat trials and in general more accurate after stimulus presentation in the LVF. This right-hemispheric dominance indicates that participants may have solved this task without in-depth verbal processing and may instead have relied on an analysis of spatial features of the two initial letters (Vogel et al., 2003).

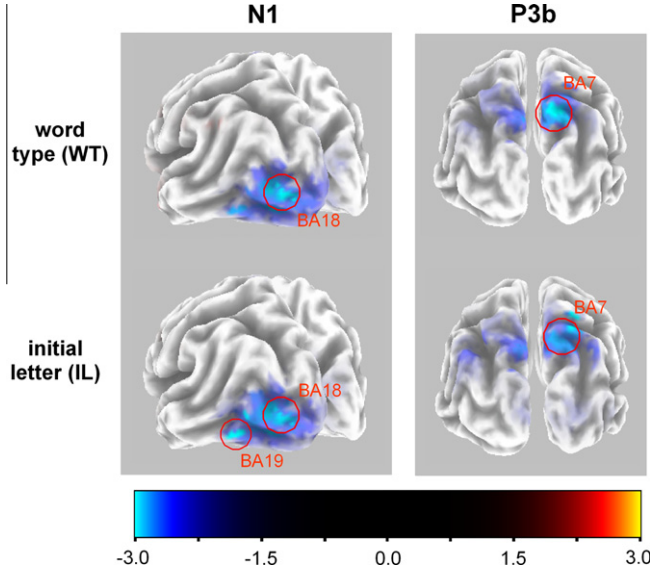

Fig. 4. Activation differences in occipital and parietal cortices causing the differences in N1 and P3b amplitudes between presenting stimuli in the LVF and RVF as revealed by sLORETA. Voxels with significant differences ($p < .01$, corrected for multiple comparisons) between LVF and RVF presentation are indicated by a colour code. Blue colour indicates that stimulus presentation in the LVF produced less activation than presentation in the RVF. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In contrast to repeat trials, no hemispheric asymmetries in reaction times were observed on switch trials in both tasks. It has been suggested that task complexity determines the degree of interhemispheric interaction with increasing task complexity resulting in greater coupling between the two hemispheres (Banich & Belger, 1990; Bayer et al., 2008; Weissman & Banich, 2000). Switch trials are more complex than repeat trials as they include additional cognitive processes including prospective reconfiguration processes, active control processes, as well as passive task interference processes (Rushworth et al., 2005). Therefore, the present results suggest that the hemispheres must interact to a greater extent in order to solve the task on switch trials. This greater interaction could lead to a reduction of hemispheric asymmetry effects in switch trials, relative to repeat trials. Moreover, this finding is also in accordance with a study that investigated the relationship of task complexity and the degree of hemispheric asymmetries in the motor domain (Hausmann et al., 2004). In this study, increasing task complexity was related to a reduction of asymmetries. While the present study did not investigate manual asymmetries but lateralisation in word processing, our findings suggest that a similar relationship exists for this asymmetry. Another important variable in this regard is the presentation time of cue and stimulus. Due to the complexity of the task used in the present study, it was necessary to use a stimulus presentation time of 185 ms in order to avoid too high error rates. It has repeatedly been shown that reliable visual field advantages can be obtained in visual half-field paradigms with this stimulus presentation time (e.g. Hausmann, Becker, Gather, & Güntürkün, 2002; Hausmann & Güntürkün, 2000) or even 200 ms (Hunter & Brysbaert, 2008; Van der Haegen, Cai, Seurinck, & Brysbaert, 2011). However, there is also some evidence suggesting that visual field advantages can be reduced when stimulus presentation time is over 150 ms, since in this case saccadic eye movements can lead to stimulus perception in both visual fields instead of one (Hardyck, Dronkers, Chiarello, & Simpson, 1985). One could speculate that especially in the more complex switch condition such effects may have lead to a reduction of hemispheric asymmetries in the behavioural data.

In the ERP data, we observed an overall left lateralization of the N1, that is, a stronger negativation of the N1 over the left hemisphere (at electrode PO7) than over the right hemisphere (at electrode PO8). This is in accordance with other studies on N1 asymmetries for visually presented words (Grossi et al., 2010; Proverbio et al., 2002; Spironelli & Angrilli, 2007). A left lateralization of the N1 was also reflected in the sLORETA analysis. Here, it was reflected by activation differences in the left extrastriate cortex with stimulus presentation in the LVF producing less activation than presentation in the RVF, a finding that further supports the assumption that the N1 is generated in the extrastriate cortex (Gomez-Gonzalez et al., 1994; Herrmann & Knight, 2001). The overall N1 asymmetry was modulated by the visual field in which the stimulus was presented. At both electrodes, the N1 was more negative after stimulus presentation in the contralateral visual field. This is in accordance with the findings of an earlier study (Johannes, Münte, Heinze, & Mangun, 1995) which also reported a more pronounced N1 after stimulus presentation in the contralateral, compared to the ipsilateral visual field using vertical bars of different sizes as stimuli. With verbal stimuli, we observed a much more pronounced dissociation between contra- and ipsilateral stimulation in the left compared to the right hemisphere. Moreover, contralateral stimulation in the left hemisphere evoked

a more pronounced N1 than contralateral stimulation in the right hemisphere. These findings suggest a left-hemispheric specialisation for processing of verbal stimuli at a very early stage of information processing. However, it has to be taken into account that activity in the extrastriate cortex is not independent of higher cognitive processes and can for example by modulated by control mechanisms for local or global attention (Sasaki et al., 2001).

For the P3b, we observed a greater positivity after stimulus presentation in the RVF compared to the LVF. In accordance with the frequently reported parietal scalp distribution of the P3b (Gajewski et al., 2010; Hsieh, 2006) this asymmetry was driven by bilateral activation differences in the superior parietal cortex with stimulus presentation in the RVF producing more parietal activation than presentation in the LVF. This finding is in line with the assumption, that the amplitude of the P3b is linked to processing capacity available for allocation of attention to on-going tasks (Polich, 2007). While the P3b itself is mediated by bilateral parietal activity, less efficient initial sensory processing of verbal stimuli in the non-dominant right hemisphere leads to a smaller P3b amplitude compared to initial sensory processing in the dominant left hemisphere since it places increased demands on cognitive processes related to stimulus evaluation that are reflected by the P3b. These results show for the first time that FCAs for the processing of verbal stimuli (as reflected by a left lateralization of the N1) affect the neurophysiological correlates of executive functions related to task switching even if these correlates are controlled bilaterally. Moreover, a greater positivity of the P3b on switch compared to repeat trials was observed in the present study. This finding is in line with several other studies using cued task switching paradigms in which the data were analysed cue-locked (Barcelo et al., 2006; Jost et al., 2008; Nicholson et al., 2005; Nicholson et al., 2006), but is in contrast to some studies in which the ERP data were analysed target-locked (Rushworth et al., 2005). Since cue and target were presented at the exact same time point in the present study, cue switch and task switch effects on the P3b were merged in the present data. Thus, our findings suggest that the cue switch is more relevant for the P3b amplitude than the task switch, at least when task complexity is low. This assumption is also in line with a recent study (Gajewski et al., 2010) that used different types of task switching paradigms. While these authors observed a reduction of the P3b in switch compared to repeat trials in a memory based task switching paradigm, their findings in a cue-based task switching paradigm were comparable to those of the present study. Here, a non-significant trend towards of greater positivity of the P3b in switch compared to repeat trials was observed. To clarify the exact relation of cue switch and task switch effects on the P3b in a tachistoscopic cued switch task, it would be an interesting follow-up study to the present study to run a similar experiment in which cue-target intervals are systematically varied, so that cue and target effects on the P3b can be dissociated.

In summary, FCAs affect the neurophysiological correlates of executive functions related to task switching on two different levels. First, FCAs for a specific type of stimuli are reflected by a lateralization of the N1, an early attentional ERP component. Moreover, initial sensory processing in the hemisphere that is non-dominant for the processing of a specific type of stimuli places increased demands on cognitive processes related to stimulus evaluation. This is reflected by a right-sided reduction of the P3b, a late ERP-component that is mediated by bilateral parietal activity.

Importantly, the study further shows that asymmetries in the neurophysiological correlates of executive functions related to task switching are not necessarily reflected by asymmetries in behavioural performance. Behavioural measures (e.g. reaction times and error rates in the present study) are an indicator of the final outcome of cognitive processing in the brain (e.g. the initial letter or the word type of the stimulus is successfully recognised, or not). ERP measures, in contrast, reflect the neuronal correlates of distinct cognitive sub-processes that occur during this process (de Haan & Nelson 1997). In the present study, neurophysiological asymmetry effects were observed for cognitive processes reflected by the N1 which are related to orient attention towards visual stimuli (Beste et al. 2008; Beste et al., 2010; Herrmann & Knight, 2001; Hillyard & Anllo-Vento, 1998; Wascher & Beste, 2010) or categorisation of these stimuli (Grossi et al., 2010). Moreover, neurophysiological asymmetry effects were also found for memory guided stimulus evaluation processes as reflected by the P3b (Kok, 2001). Thus, the dissociation between neurophysiological and behavioural asymmetries observed in the present study implies that other cognitive processes also play a role for behavioural asymmetries in tachistoscopic task switching paradigms. For example, it has been shown that hemispheric asymmetries on the behavioural level can be influenced by instructing participants to allocate attention to specific stimuli (Westerhausen et al., 2009).

In the present study, participants may have allocated attention to spatial aspects of the stimuli when they had to conduct the initial letter task, but to semantic aspects when they had to conduct the word type task. These strategy-specific attentional allocation differences are not reflected by the ERP components investigated in the present study and may therefore explain the dissociation between ERP and behavioural data. However, more research is needed to verify this theory. In accordance with earlier findings (Banich and Belger, 1990; Bayer et al., 2008; Weissman and Banich, 2000) the data suggest that task complexity influences behavioural asymmetries, with more complex tasks leading to less asymmetry in behavioural measures, possibly due to increased interhemispheric interaction. In conclusion, our findings suggest that FCAs should be considered as an important modulator variable when investigating executive functions.

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