

Response inhibition to emotional faces is modulated by functional hemispheric asymmetries linked to handedness

Elisabeth Schrammen^a, Gina M. Grimshaw^b, Adam M. Berlijn^c, Sebastian Ocklenburg^{d,1}, Jutta Peterburs^{a,c,*,1}

^a Institute of Medical Psychology and Systems Neuroscience, University of Münster, Germany

^b School of Psychology, Victoria University of Wellington, New Zealand

^c Biological Psychology, Institute of Experimental Psychology, Heinrich-Heine-University Düsseldorf, Germany

^d Biopsychology, Institute of Cognitive Neuroscience, Department of Psychology, Ruhr-University Bochum, Germany

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ABSTRACT

Effective response inhibition requires efficient bottom-up perceptual processing and effective top-down inhibitory control. To investigate the role of hemispheric asymmetries in these processes, 49 right- and 50 left-handers completed a tachistosopic Go/Nogo task with positive and negative emotional faces while ERPs were recorded. Frontal resting state EEG asymmetry was assessed as a marker of individual differences in prefrontal inhibitory networks. Results supported a dependency of inhibitory processing on early lateralized processes. As expected, right-handers showed a stronger N170 over the right hemisphere, and better response inhibition when faces were projected to the right hemisphere. Left-handers showed a stronger N170 over the left hemisphere, and no behavioural asymmetry. Asymmetries in response inhibition were also valence-dependent, with better inhibition of responses to negative faces when projected to the right, and better inhibition of responses to positive faces when projected to the left hemisphere. Frontal asymmetry was not related to handedness, but did modulate response inhibition depending on valence. Consistent with the asymmetric inhibition model (Grimshaw & Carmel, 2014), greater right frontal activity was associated with better response inhibition to positive than to negative faces; subjects with greater left frontal activity showed an opposite trend. These findings highlight the interplay between bottom-up and top-down processes in explaining hemispheric asymmetries in response inhibition.

1. Introduction

In our daily lives we often need to override a habitual or prepotent response so we can achieve our goals. Such *response inhibition* can be particularly challenging when the triggers for our actions are emotional. Moreover, deficits in inhibiting a response to certain emotional information have been linked to psychopathology, e.g. depression (Goeleven, de Raedt, Baert, & Koster, 2006). Successful inhibition of a response depends on the interplay between bottom-up factors that determine the strength of the behavioural trigger, and the top-down implementation of inhibitory control. Both pathways have been shown to depend on lateralized brain networks, with hemispheric asymmetries in sensory, affective, and perceptual processing affecting the bottom-up pathway (Ocklenburg, Güntürkün, & Beste, 2011), and asymmetric activation in lateral prefrontal regions underpinning effective

inhibitory control (Aron, Robbins, & Poldrack, 2004).

Much of what we know about these asymmetries is based on research with right-handers, because left-handers are commonly excluded from neuroscience research for the sake of sample homogeneity (Willems, Peelen, & Hagoort, 2010). This is of course a problem for the generalisability of conclusions and a lost opportunity because left-handers differ from right-handers in many aspects of lateralized processing, e.g., self-body recognition (Morita, Asada, & Naito, 2020), language and spatial attention (e.g., O'Regan & Serrien, 2018; van der Haegen & Brysbaert, 2018), and face and body processing in the visual system (Willems et al., 2010). Along these lines, investigating left-handers may yield unique insights into brain-behaviour relationships. In the present study, we used the natural variation in hemispheric asymmetry provided by studying both left- and right-handers to investigate the lateralized processes that support effective response

* Corresponding authors at: Department of Biological Psychology, Institute of Experimental Psychology, Heinrich-Heine-University Düsseldorf, Germany.
E-mail address: Jutta.Peterburs@hhu.de (J. Peterburs).

¹ These authors contributed equally.

inhibition.

In the lab, response inhibition is most commonly assessed using the Go/Nogo paradigm (Aron, 2007; Beck, Bransome, Mirsky, Rosvold, & Sarason, 1956). In a typical task, participants are asked to respond to one kind of stimulus (the Go-stimulus) as quickly as possible, while withholding response to another kind (the Nogo-stimulus). In most experimental designs, a Go-response is demanded on the majority of trials, resulting in a prepotent tendency to respond and the need to recruit regulatory control to actively inhibit that response when the Nogo-stimulus is presented (e.g., Aron, 2007; Jones, Cho, Nystrom, Cohen, & Braver, 2002). As mentioned above, effective inhibitory control is especially relevant in the presence of emotional content (e.g., Padmala, Bauer, & Pessoa, 2011). Therefore, in the present study, we used emotional faces as the Go- and Nogo-stimuli to probe the mechanisms of inhibitory control under emotional conditions.

Behaviourally, the main measure of interest is the false alarm rate, reflecting the extent to which a person fails to inhibit a response. Along these lines, good inhibitory control will result in fewer false alarms than poor inhibitory control. Successful inhibition is also reflected in neuronal indices. In neuroimaging and patient studies, inhibitory control as elicited by the Go/Nogo-task is often localised to regions of the lateral prefrontal cortex (Casey et al., 1997; Chikazoe, 2010). In electrophysiological studies, two components of the event-related potential (ERP) have been associated with inhibitory control: the Nogo-N2 and the Nogo-P3. The Nogo-N2 is a negative peak in fronto-parietal areas within 200–300 ms after stimulus presentation that is typically found to be enhanced (i.e., more negative) in Nogo- compared to Go-trials (Eimer, 1993; Gemba & Sasaki, 1989; Jodo & Kayama, 1992; Pfefferbaum, Ford, Weller, & Kopell, 1985). The Nogo-N2 is commonly assumed to reflect inhibitory processes (Band & van Boxtel, 1999; Eimer, 1993), with more negative amplitudes related to better inhibitory performance, e.g., lower false alarm rates (Falkenstein, Hoormann, & Hohnsbein, 1999) and faster responses (van Boxtel, van der Molen, Jennings, & Brunia, 2001). The Nogo-P3 is a positive deflection that peaks within 300–600 ms after stimulus presentation and is also found to be more pronounced on Nogo- compared to Go-trials (Eimer, 1993). In contrast to the Nogo-N2, which is assumed to reflect the main phase of the inhibitory process (e.g., response inhibition), the later occurring Nogo-P3 is argued to reflect post-response processes (Bokura, Yamaguchi, & Kobayashi, 2001; Roche, Garavan, Foxe, & O'Mara, 2005) such as evaluation of successful inhibition, error detection, and/or context updating (Roche et al., 2005).

From a bottom-up perspective, effective response inhibition depends on efficient processing of incoming sensory signals, which may depend on the hemisphere that dominates perceptual processing. As shown throughout a long history of neuroscientific research, the left and right hemisphere exhibit different functional specializations, and these functional hemispheric asymmetries can be observed for numerous cognitive abilities (for a comprehensive review, see Ocklenburg & Güntürkün, 2018). Whereas processing of language, for example, relies heavily on the left hemisphere (Vigneau et al., 2006), processing of faces seems to particularly engage the right hemisphere (Levine, Banich, & Koch-Weser, 1988; Rossion, Joyce, Cottrell, & Tarr, 2003). Given that response inhibition is modulated by bottom-up factors, the ability to inhibit a response might be influenced by the hemisphere that initially processes the Go or Nogo stimulus. Indeed, findings from Measso and Zaidel (1990) as well as from Ocklenburg et al. (2011) suggest that responses to words initially processed within the language-dominant left hemisphere are better inhibited than responses to words initially processed within the non-dominant right hemisphere. Similarly, initial processing of faces in the face-dominant right hemisphere facilitates behavioural and neural indices of response inhibition (Ocklenburg, Ness, Güntürkün, Suchan, & Beste, 2013), indicating that this principle is not specific to the language domain.

Compared to right-handers, left-handers often show reduced, or even reversed, functional asymmetries (Knecht et al., 2000). For

example, although most left-handers have the same left hemisphere specialization for language processing as right-handers, as a group they are less lateralized, and individuals are more likely to demonstrate a reversed right hemisphere specialization (e.g., Knecht et al., 2000). Similar differences are observed in face processing, with left-handers showing less pronounced right – or even left – hemispheric dominance (Badzakova-Trajkov, Häberling, Roberts, & Corballis, 2010; Willems et al., 2010). If our assumption is correct that response inhibition is modulated by hemispheric differences in early stages of processing, differing hemispheric asymmetries in right- and left-handers should modulate their inhibitory performance accordingly.

To examine the consequences of early visual lateralization on behavioural and neural indices of inhibitory control, we restricted initial processing to one hemisphere through tachistoscopic presentation of visual stimuli (Bourne, 2006), i.e., the Go or Nogo stimulus was briefly presented in either the left or right visual field (RVF; LVF). Given the anatomy of the visual pathway, visual stimuli presented in the LVF are initially processed in the right hemisphere, while stimuli presented in the RVF are initially processed in the left hemisphere. To examine laterality for face processing in our sample of left- and right-handers, we used the N170, an ERP component linked to the encoding of faces (Herrmann, Ehlis, Ellgring, & Fallgatter, 2005; Rossion et al., 2003). If tachistoscopic presentation works as intended, we would expect a more negative N170 over the right hemisphere after LVF presentation, and a more negative N170 over the left hemisphere after RVF presentation. Additionally, assuming right hemispheric dominance for faces in right-handers, for the right-handed participants we expected a more negative N170 overall over the right hemisphere than over the left. Assuming less pronounced right (or potentially even left) hemispheric dominance in left-handers, for the left-handed participants we would expect a less pronounced N170 over the right hemisphere (or potentially even a more pronounced N170 over the left).

If this hemispheric difference in early face processing affects subsequent inhibitory control, we should expect to see fewer false alarms in right-handers after processing the faces within the dominant right hemisphere (LVF presentation), while for left-handers we would expect no lateral differences, or potentially even fewer false alarms after processing in the left hemisphere (RVF presentation). Likewise, for the Nogo-N2, we expected right-handers to show increased negativity after processing in the non-dominant left hemisphere (reflecting greater conflict), while for left-handers we expected this laterality effect to be less pronounced or even a reversed effect. Finally, as an index of successful inhibition, the Nogo-P3 for right-handers should be stronger after initial processing in the dominant right hemisphere, while again for left-handers we would expect a less pronounced or even reversed laterality effect.

In addition to these hemispheric asymmetries in bottom-up stimulus processing, top-down response inhibition is also suggested to depend on trait asymmetries in prefrontal activation (Aron et al., 2004; Gable et al., 2015, 2018; Grimshaw & Carmel, 2014). In EEG studies, this frontal asymmetry (FA) can be measured by comparing alpha power generated by left versus right frontal cortices during a resting phase. Alpha power (visible as 8–12 Hz frequency in the EEG) is assumed to reflect the inverse of regional neuronal activity, so less alpha power over right than left frontal cortices indicates greater right frontal activity (FA), and less alpha power over left than right frontal cortices indicates greater left FA (e.g., Coan & Allen, 2004; Cook, O'Hara, Uijtdehaage, Mandelkern, & Leuchter, 1998; Davidson, Chapman, Chapman, & Henriques, 1990). Stable, individual differences in resting state FA have been linked to a number of cognitive, affective, and personality factors (e.g., Harmon-Jones & Gable, 2018; Keune, Mayer, Jusyte, & Schönenberg, 2018; Thibodeau, Jorgensen, & Kim, 2006). With respect to inhibitory control, two models suggest a relationship between FA and response inhibition. The revised behavioural inhibition model (r-BIS) associates the right frontal hemisphere with a regulatory control system, and thus predicts that greater rightward FA should

result in better inhibitory performance (Aron et al., 2004; Gable et al., 2015, 2018). In contrast, the asymmetric inhibition model (AIM; Grimshaw & Carmel, 2014) suggests that hemispheric differences in inhibitory control are modulated by valence, with greater right FA associated with better inhibition of positive information, and greater left FA associated with better inhibition of negative information. Our experimental paradigm allows us to test the predictions arising from both models. If the r-BIS is valid, we would expect a main effect of frontal asymmetry on inhibitory performance, i.e., greater rightward FA should be associated with fewer false alarms. According to the AIM, we would expect an interaction of frontal asymmetry and valence on inhibitory performance, i.e., greater rightward FA should be associated with fewer false alarms in response to positive versus negative stimuli, and greater leftward FA should be associated with fewer false alarms in response to negative versus positive stimuli.

Concerning handedness, little is known about FA in left- versus right-handers. Some findings suggest that in comparison to consistent right-handers, participants with no clear hand preference show greater right frontal activity (Ocklenburg et al., 2019; Propper, Pierce, Geisler, Christman, & Bellorado, 2012). In the absence of a clear theoretical rationale, we consider analyses involving handedness to be exploratory.

2. Methods

2.1. Sample

In total, 106 participants took part in the experiment, of which seven had to be excluded due to the following reasons: incomplete data sets because of technical problems (three), current intake of antidepressants (one), insufficient EEG data quality (two), and task performance at chance level based on d' values (one). The final sample of 49 self-reported right-handers (35 women and 14 men, mean age = 25.57 years, $SD = 6.45$, range 19–54 years) and 50 self-reported left-handers (35 women and 15 men, mean age = 23.28 years, $SD = 3.00$, range 19–31 years) did not currently suffer from any psychological or neurological disorders, was free of psychotropic medication, and had normal or corrected-to-normal vision. Right- and left-handers did not differ according to depression scores measured with the German adaptation (Hautzinger, Keller, & Kühner, 2006) of the *Beck Depression Inventory-II* (BDI-II; Beck, Steer, & Brown, 1996; mean score right-handers = 4.75, $SD = 4.27$; mean score left-handers = 4.82, $SD = 4.11$), or intelligence level, as assessed with the *Mehrfachwahl-Wortschatz-Intelligenztest*, MWT-B, Lehrl, 1999; both $p > .594$). BDI and MWT-B are established and widely used tests in Psychological research and both yield high re-test reliability (BDI: 0.93 according to Beck et al., 1996; MWT-B: 0.87 according to Blaha & Pater, 1979).

In addition to self-reported handedness, the *Edinburgh Handedness Inventory* (Oldfield, 1971) was administered to control for strength and consistency of hand preferences as potential confounds. The EHI is self-report questionnaire with items asking for the preferred hand for carrying out 10 common activities such as writing, throwing a ball, and using a toothbrush. Subjects rate their hand preferences by choosing one of five options: “always left (+2 left)”, “mostly left (+1 left)”, “both equally (+1 left, plus +1 right)”, “mostly right (+1 right)”, or “always right (+2 right)”. Based on the answers, a laterality quotient is calculated based on the number of activities carried out with the right (R) versus with the left hand (L) according to the following formula: $(R-L)/(R+L)*100$. EHI scores can range from -100 (strong left-handedness) to 100 (strong right-handedness), with scores between -60 and 60 indicating no clear hand preference, i.e., mixed-handedness (Isaacs, Barr, Nelson, & Devinsky, 2006). For EHI, an overall re-test reliability of 0.97 has been reported but this value may be misleading because re-test reliability was shown to differ for specific subgroups, with 0.86 for right- and 0.76 for left-handers (McMeekan & Lishman, 1975). In the present sample, the EHI scores indicated 45 strong right-handers, 29 strong left-handers and 25 mixed-handers (4 right- and 21 left-

handers).

Participants were recruited with advertisements and flyers distributed at the University of Münster, Germany, and in social networks and received either 16 € or course credit for participation. Written informed consent was obtained prior to starting the experiment. Sample size in the present study is in line with other work on handedness and cognitive functions (e.g., Morita et al., 2020; Polich & Hoffman, 1998), and takes into account more difficult recruitment of left-handers because they make up only about 10% of the population, as confirmed also in a large, recent meta-analysis (Papadatou-Pastou et al., 2020).

The present study was conducted in compliance with the ethical principles for human subjects research outlined in the Declaration of Helsinki and received ethical clearance by the institutional ethics committee of the Faculty of Psychology at Ruhr-University Bochum, Germany.

2.2. Procedure

After giving informed consent, participants completed a demographic questionnaire and the EHI. EEG was set up according to standard protocol. In the first part of the experiment, alpha power was assessed during a four-minute resting period, two minutes with eyes open (O) and two minutes with eyes closed (C), in alternating one-minute blocks. Two different sequences (O-C-C-O and C-O-O-C) were used and balanced across the sample. Four minutes of resting EEG have been shown to provide enough data to reliably assess alpha asymmetry (Allen, Coan, & Nazarian, 2004; Allen, Urry, Hitt, & Coan, 2004; Smith, Reznik, Stewart, & Allen, 2017). Slightly better reliability of alpha asymmetry is also obtained when combining epochs of eyes open and eyes closed, instead of only using one measure (Hagemann, Naumann, Becker, Maier, & Bartussek, 1998).

Next, participants completed the Go/Nogo-task that consisted of 2176 trials in total, coded and presented using *Presentation* software (Version 17.2, Neurobehavioral Systems, Inc., Berkeley, CA, USA). Stimuli were presented on a 17" CRT monitor with a refresh rate of 60 Hz.

As illustrated in Fig. 1, each trial of the Go/Nogo-task started with the presentation of an emotional face presented tachistoscopically for 185 ms, followed by a fixation cross for 365 ms and an inter-trial interval (ITI) ranging from 750 to 950 ms. Participants were instructed to focus on the fixation cross throughout the task and to respond as quickly and as accurately as possible. The stimuli were two male faces (Thoma, Soria Bauser, & Suchan, 2013), one with an angry and one with a friendly facial expression. Participants sat at a viewing distance of 57 cm in front of a 17-in. monitor with their heads placed on a chin rest. The faces had a width of 3° and a height of 5° and were presented at an eccentricity of 5° of visual angle (to the center of the stimulus). Tachistoscopic face presentation was randomized, with the requirement that participants saw an equal number of faces presented in the left (LVF) and right visual field (RVF). The Go/Nogo-task was divided into two blocks. In Block A, the angry face served as the Go-stimulus, and

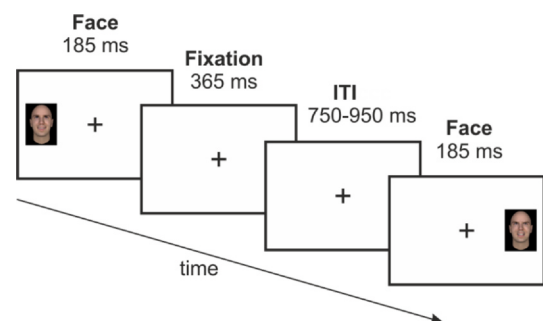


Fig. 1. Schematic illustration of the time course of stimulus presentation in the tachistoscopic Go/Nogo task.

participants were instructed to respond by button press whenever they saw the angry face. The friendly face served as the Nogo-stimulus in response to which responses had to be withheld. In Block B, Go- and Nogo-stimuli were reversed, thus the friendly face served as the Go-stimulus and the angry face as the Nogo-stimulus. In both blocks, 70% of trials were Go- and 30% were Nogo-trials. Block order was balanced across the sample. A short break was inserted between blocks to reduce errors due to the switching of Go- and Nogo-stimuli in which participants completed BDI and MWT-B. Within each block, participants completed half of the trials responding with their left, and the other half responding with their right index finger in order to control for artifacts due to motor responses. For analysis, trials from both hands were collapsed.

2.3. EEG data recording and preprocessing

EEG data were recorded with a sampling rate of 512 Hz using a 64-channel active electrode set (BioSemi, Amsterdam, The Netherlands). Additionally, four external electrodes were used to record horizontal and vertical eye movements to later correct for ocular artefacts. All electrode impedances were kept below 5 k Ω . Off-line analyses were conducted using *BrainVision Analyzer 2* (Version 2.1.1.327; Brain Products GmbH, Munich, Germany). In keeping with the procedures used in a previous study (Ocklenburg et al., 2013), data were filtered with a 0.5 Hz low-pass, a 20 Hz high-pass filter, and a 50 Hz notch filter. Of note, there is evidence that heavy low-cutoff filters can introduce artifacts that present as an early negativity (Tanner, Morgan-Short, & Luck, 2015; Tanner, Norton, Morgan-Short, & Luck, 2016). However, since filtering in the present study was applied prior to separating the experimental conditions, the filter was unlikely to differentially affect conditions and thus be a confound for early ERP negativities such as the N170 (see below). After re-referencing to the average of electrodes P7, P8, T7, T8, TP7, and TP8, ocular artifacts were corrected using *ocular correction independent component analysis* (ICA; using the infomax algorithm) as implemented in *BrainVision Analyzer 2*, and visually inspected for correctness. Automatic raw data inspection was performed in order to reject intervals with potential artefacts reflected in amplitudes higher or lower than $\pm 200 \mu\text{V}$ and in amplitude differences exceeding $200 \mu\text{V}$ in 200 ms intervals.

Assessing ERPs. After ICA, EEG data recorded during the Go/Nogo-task were segmented into 1500 ms epochs time-locked to Go- and Nogo-stimulus presentation (covering 200 ms before and 1300 ms after presentation). Only trials with correct responses (or correctly withheld responses) were used for further analysis. After baseline correction based on the 200 ms immediately preceding stimulus presentation, automated artifact rejection was applied to the epoched data as specified above. For all included participants, at least 80% of trials remained for analysis. Segments were averaged according to condition (Go/Nogo), valence (positive/negative), and visual field (LVF/RVF). Using *MATLAB* (The MathWorks Inc., Natick, MA, USA), automatic peak detection was applied for identifying ERP components as follows. Time windows and electrode sites for ERP analyses were determined based on both visual inspection of the grand-average waveforms and on the procedures applied in a previous study in which the same experimental task was used (Ocklenburg et al., 2013), in order to enhance comparability of the findings. For the N2, the local minimum within a time window of 200–400 ms after stimulus presentation was detected at electrode FCz (see also Bekker, Kenemans, & Verbaten, 2005). The P3 was calculated relative to the N2 (see also Peterburs, Liepelt, Voegler, Ocklenburg, & Straube, 2019). First, the local maximum at FCz was identified within 250–550 ms after stimulus presentation. Then, the peak-to-peak amplitude difference between the local maximum and the preceding local minimum was calculated. Of note, in an additional, explorative analysis reported as supplemental material, P3 amplitudes were also scored as maximum positive peak at electrode Pz 300–500 ms post-stimulus.

Of note, the optimal sites for N170 quantification have been a matter of debate, with some researchers recommending to use PO8/PO7 because N170 peak and face-object differentiation decrease considerably at more medial occipital, temporal, or parietal locations (e.g., Rossion & Jacques, 2008). However, grand average waveforms and scalp topographies in the present study revealed that the N170 was most pronounced at electrodes CP5 and CP6. For this reason, and in keeping with Ocklenburg et al. (2013), automatic peak detection was used to identify the local minimum at electrodes CP5 and CP6 within a time window of 100–200 ms post-stimulus.

Extracting Alpha Asymmetry. To achieve a reference-free evaluation, current source density (CSD) of the signals was performed (Perrin, Pernier, Bertrand, & Echallier, 1989). This procedure has been recommended when 60 or more channels are used (Smith et al., 2017). After preprocessing, resting state EEG data were segmented into four one-minute blocks, and each block into 1.024 sec epochs (with 50% overlap in order to apply a 10% Hemming-window during frequency extraction). Artifacts were rejected using the following criteria: the maximal allowed voltage steps were 50 $\mu\text{V}/\text{ms}$, the maximal allowed difference of values was 200 μV in a 200 ms interval, and the lowest allowed activity was 0.1 μV . To extract alpha power, a fast Fourier transformation with a 10% Hemming-window was used. Windowing prevents discontinuity in the signal that would lead to artifactual frequencies when using Fourier transformation (Allen, Coan, et al., 2004). Individual asymmetry scores were calculated by subtracting the natural log-transformed mean alpha power averaged over left frontal electrodes (F3, F5, and F7) from the similarly transformed alpha power averaged over right frontal electrodes (F4, F6, and F8), i.e., $\ln(F4 F6 F8) - \ln(F3 F5 F7)$.

2.4. Statistical analysis

Statistical Analyses were conducted using IBM SPSS Statistics (Statistical Product and Service Solution; SPSS Inc., Chicago, IL, USA). For each dependent variable (false alarm rates, N170, N2, and P3 amplitude), a 2-level Hierarchical Linear Model (HLM) was calculated. Specifically, our data (Level1-units; i.e., dependent variables according to condition (Go/Nogo), valence (positive/negative), and visual field (LVF/RVF)) were nested in participants (Level2-units with the Level2-predictors handedness (right/left) and individual frontal activity index). Since we were mostly interested in cross-level interactions, e.g., how the Level2-predictor handedness influenced the effect of the Level1-predictor visual field on the dependent variable (e.g., false alarm rate), we followed the guidelines outlined by Aguinis, Gottfredson, and Culpepper (2013). For all models, categorical predictors were effect-coded (see Table 1 for the coding scheme). Centering of the only metric predictor (frontal asymmetry) was not necessary, since natural log-transformation was already applied when calculating the asymmetry scores, giving the scores a meaningful zero value (Aguinis et al., 2013). Degrees of freedoms (*df*) were estimated using Satterthwaite's technique (Satterthwaite, 1941) and rounded to the full number when reported. Differences in frontal asymmetry between right-, left-, and mixed-handers were examined using a one-way analysis of variance (ANOVA). Alpha level for all analyses was set at 0.05.

Table 1
Effect coding scheme.

Code	-1	1
Valence	Negative	Positive
Visual Field	LVF	RVF
Handedness	Left	Right
Condition	Go	Nogo
Electrode	CP5	CP6

Note. LVF = left visual field, RVF = right visual field.

Table 2
Regression table for N170 amplitudes –fixed and random effects.

Parameter	b	SE	t (df)	p	η^2
Intercept	-1.97	0.09	-22.35 (99)	< 0.001***	0.835
Frontal Asymmetry	-0.33	0.18	-0.19 (99)	0.85	0.000
Handedness	0.06	0.09	0.65 (99)	0.52	0.004
Valence	-0.01	0.02	-0.52 (1287)	0.61	0.001
Visual Field	-0.01	0.04	-0.18 (99)	0.86	0.000
Condition	-0.03	0.02	-1.09 (1287)	0.28	0.001
Electrode	-0.01	0.07	-0.08 (99)	0.93	0.000
Valence*Visual Field	-0.02	0.02	-0.95 (1287)	0.35	0.001
Valence*Condition	-0.01	0.02	-0.33 (1287)	0.74	0.000
Visual Field*Condition	0.01	0.02	0.49 (1287)	0.62	0.000
Valence*Electrode	0.01	0.02	0.63 (1287)	0.53	0.000
Visual Field*Electrode	0.78	0.02	33.97 (1287)	< 0.001***	0.473
Condition*Electrode	0.00	0.02	0.20 (1287)	0.84	0.000
Frontal Asymmetry*Handedness	-0.02	0.18	-0.13 (99)	0.90	0.000
Frontal Asymmetry*Valence [†]	-0.00	0.05	-0.02 (1287)	0.98	0.000
Frontal Asymmetry*Visual Field [†]	0.00	0.09	0.01 (99)	0.99	0.000
Frontal Asymmetry*Condition [†]	0.02	0.05	-0.40 (1287)	0.69	0.000
Frontal Asymmetry*Electrode [†]	0.29	0.15	1.91 (99)	0.06	0.036
Handedness*Valence [†]	0.01	0.02	0.44 (1287)	0.66	0.000
Handedness*Visual Field [†]	0.07	0.04	1.73 (99)	0.09	0.029
Handedness*Condition [†]	0.01	0.02	0.33 (1287)	0.75	0.000
Handedness*Electrode [†]	-0.21	0.07	-2.93 (1287)	< 0.01**	0.080

Variance Components	Estimate	SE
Residual	0.84	0.03
Intercept	0.71	0.11
Slope Electrode	0.47	0.07
Slope Visual Field	0.13	0.03
Cor(Intercept*Slope Electrode)	0.12	0.11
Cor(Intercept*Slope Visual Field)	0.23	0.12
Cor(Slope Visual Field*Slope Electrode)	0.15	0.12

Note. b = regression coefficient; SE = standard error; df = degrees of freedom; η^2 = semi-partial R²; Cor = Correlation; [†]Cross-level interactions. Df rounded to full number and η^2 to third decimal. All other values rounded to second decimal.

3. Results

Regarding overall task performance, participants showed a mean response time of 517 ms (*SD* = 61) in Go-trials, with a mean hit rate of 86.88% (*SD* = 11.09). The correct rejection rate was 77.01% (*SD* = 13.12). Self-reported left- and right-handers did not differ significantly in overall task performance (left-handers: mean response time = 510 ms (*SD* = 61), mean hit rate = 88.72 (*SD* = 10.20), mean false alarm rate = 23.13 (*SD* = 13.34); right-handers: mean response time = 526 ms (*SD* = 61), mean hit rate = 84.98 (*SD* = 11.74), mean false alarm rate = 22.84 (*SD* = 13.02); all *p* > .094). The ANOVA revealed that right-, left-, and mixed-handers (according to EHI scores) did not differ in frontal asymmetry (mean right-handers = -0.035, *SD* = 0.467; mean mixed-handers = 0.067, *SD* = 0.531; mean left-handers = 0.109, *SD* = 0.480; *F*(2, 96) = 0.848, *p* = .431). When ignoring strength of hand-preference by only comparing asymmetry scores between right- and left-handers based on self-report, there was also no difference observed (*t*(97) = -0.892, *p* = .375).

N170. Fixed and random effects parameters for the final HLM on N170 amplitude are shown in Table 2. Grand-average stimulus-locked ERPs according to condition (Go/Nogo), valence (positive/negative), and visual field (LVF/RVF) at electrodes CP5 and CP6 are provided in Fig. 3 separately for left- (Fig. 3A) and right-handers (Fig. 3B). In addition, scalp topographies at the time point of peak negativity in the

N170 time window are provided according to visual field and handedness.

The Intraclass Correlation Coefficient (ICC) of ρ = 0.22 was highly significant (*t*(1584) = 8.97, *p* < .001), making the use of a hierarchical regression model necessary. Random slope effects for visual field and electrode were significant, so both were included in the final model. At the lowest level, the final model reduced the prediction error of N170 amplitude to a large degree with Pseudo-R₁² = 0.45. At the second level, the model hardly reduced the prediction error of N170 amplitude for any participant (Pseudo-R₂² = 0.004). We found the expected interaction of visual field and electrode on N170 amplitude. Simple slope analysis revealed that the N170 was more negative at right-hemispheric CP6 after face presentation in the LVF (*b* = -0.79, *SE* = 0.08, *t*(119.73) = -10.33, *p* < .001), and more negative at left-hemispheric CP5 after face presentation in the RVF (*b* = 0.78, *SE* = 0.08, *t*(119.73) = 10.17, *p* < .001; also evident in the scalp topographies). These results confirmed that the tachistoscopic stimulus presentation had worked as intended. As expected, we found an interaction of handedness and electrode: self-reported right-handers generally showed a more negative N170 over CP6 than over CP5 (*b* = -0.22, *SE* = 0.10, *t*(99) = -2.13, *p* < .05), while self-reported left-handers showed a more negative N170 over CP5 than over CP6 (*b* = 0.21, *SE* = 0.10, *t*(99) = 2.02, *p* < .05). Excluding mixed-handers from analysis (i.e. including only strong right- and left-handers) did not alter the result patterns.

False Alarm Rate. Fixed and random effects parameters for the final HLM on false alarm rate are shown in Table 3. The ICC of ρ = 0.77 was highly significant (*t*(394) = 23.96, *p* < .001), making the use of a hierarchical regression model necessary. While the random slope effect for the Level1-predictor valence was significant, the Level1-predictor visual field did not show a variance of slopes. Thus, only the first was included in the final model. Note that we tested the cross-level interactions of interest regarding visual field (e.g., the interaction of handedness and visual field) anyway, since it is possible to have a significant cross-level interaction even when the slopes of the included Level1-predictor do not vary (Aguinis et al., 2013). At the lowest level, the model reduced the prediction error of false alarm rate to a small degree, Pseudo-R₁² = 0.11. At the second level, the model reduced the prediction error of false alarm rate for any participant to a small degree, Pseudo-R₂² = 0.06.

As expected, we found a significant interaction of handedness and visual field as illustrated in Fig. 4A. Simple slope analysis revealed that

Table 3
Regression table for false alarm rates – fixed and random effects.

	b	SE	t (df)	p	η^2
Intercept	22.91	1.30	17.60 (99)	< 0.001***	0.758
Frontal Asymmetry	4.43	2.70	1.64 (99)	0.10	0.027
Handedness	-0.00	1.30	0.00 (99)	1.00	0.000
Valence	-0.33	0.42	-0.79 (99)	0.43	0.006
Visual Field	0.48	0.27	1.79 (198)	0.08	0.016
Valence* Visual Field	-1.27	0.27	-4.68 (198)	< 0.001***	0.100
Frontal Asymmetry*Handedness	1.61	2.64	0.61 (99)	0.54	0.004
Frontal Asymmetry*Valence [†]	2.12	0.87	2.43 (99)	< 0.05*	0.056
Handedness*Valence [†]	0.44	0.42	1.03 (99)	0.31	0.011
Frontal Asymmetry*Visual Field [†]	0.48	0.56	0.85 (198)	0.40	0.004
Handedness*Visual Field [†]	0.61	0.27	2.23 (198)	< 0.05*	0.025

Variance Components	Estimate	SE
Residual	29.01	2.92
Intercept	158.73	23.61
Slope Variance	10.33	2.60
Cor(Intercept*Slope)	-0.26	0.13

Note. b = regression coefficient; SE = standard error; df = degrees of freedom; η^2 = semi-partial R²; Cor = Correlation; [†]Cross-level interactions. Df rounded to full number and η^2 to third decimal. All other values rounded to second decimal.

self-reported right-handers showed a lower false alarm rate after face presentation in the LVF than the RVF ($b = 1.09, SE = 0.38, t(198) = 2.84, p < .01$). For self-reported left-handers, there was no difference in false alarm rate between LVF and RVF presentation ($b = -0.12, SE = 0.38, t(198) = -0.32, p = .75$). Results did not change when excluding mixed-handers from analysis.

Interestingly, a significant interaction of visual field and valence was also observed (see Fig. 4B). Simple slope analysis specified that after presentation in the RVF, false alarm rates were lower for positive in comparison to negative faces ($b = -1.60, SE = 0.50, t(182) = -3.193, p < .01$), while after presentation in LVF, false alarm rates were tendentially lower for negative in comparison to positive faces ($b = 0.93, SE = 0.50, t(182) = 1.86, p = .07$). To explore if handedness might have an effect on the interaction, the three-way interaction (handedness*valence*visual field) was introduced to the equation, but did not yield significance ($b = 0.01, SE = 0.27, t(198) = 0.03, p = .979$). While there was no main effect of frontal asymmetry, the interaction of frontal asymmetry and valence reached significance. Simple slope analysis revealed that under low frontal asymmetry, valence had a negative effect on false alarm rate ($b = -1.37, SE = 0.62, t(99) = -2.21, p = .03$), indicating that lower false alarm rates for positive in comparison to negative faces were associated with negative asymmetry scores (reflecting right frontal activity). Under high frontal asymmetry, valence did not have a significant effect on false alarm rate ($b = 0.7, SE = 0.58, t(99) = 1.21, p = .23$). However, the positive beta weight indicates the opposite pattern compared to low frontal asymmetry, i.e., higher false alarm rates for positive in comparison to negative faces are associated with positive asymmetry scores (reflecting greater left frontal activity).

N2. Fixed and random effects parameters for the final HLM on N2 amplitude are shown in Table 4. The ICC of $\rho = 0.70$ was highly significant ($t(792) = 27.55, p < .001$), making the use of a hierarchical regression model necessary. Only the random slope effect for the Level1-predictor visual field was significant and thus included in the final model. At the lowest level, the model reduced prediction error of N2 amplitude to a medium degree, Pseudo- $R^2 = 0.15$. At the second level, the model did not reduce prediction error of N2 amplitude for any participant, Pseudo- $R^2 = 0.00$. Against our predictions, there was no

main effect for condition on N2 amplitude, meaning the N2 was not more pronounced in Nogo- compared to Go-trials. Similarly, the three-way interaction of interest (condition*handedness*visual field) did not reach significance. There was a main effect of valence on N2 amplitude, with a more negative N2 in trials with positive faces. There was a (marginally) significant interaction effect of visual field and condition, as well as a significant interaction effect of frontal asymmetry and condition observed. However, neither held up under simple slope testing. Excluding mixed-handers from the analysis changed results insofar that the interaction of frontal asymmetry and condition no longer yielded significance, which casts doubt on the robustness of that finding.

P3. Fixed and random effects parameters for the final HLM on P3 amplitude are shown in Table 5. The ICC of $\rho = 0.64$ was highly significant ($t(790) = 23.41, p < .001$), making the use of a hierarchical regression model necessary. The random slope effects for visual field and for condition were significant, so both were included in the final model. At the lowest level, the model reduced the prediction error of P3 amplitude to a small degree, Pseudo- $R^2 = 0.07$. At the second level, the model did not reduce the prediction error of P3 amplitude for any participant, Pseudo- $R^2 = 0.01$. The main effect of condition reached significance, with a more positive P3 amplitude for Nogo- versus Go-trials. The expected interactions regarding our hypothesis (condition*handedness*visual field) failed to reach significance. There was a significant interaction of frontal asymmetry and visual field. Simple slope testing revealed that under high (i.e., greater relative leftward) frontal asymmetry, the P3 was higher after LVF in comparison to RVF presentation ($b = -0.26, SE = 0.09, t(99) = -2.82, p < .01$). Excluding mixed-handers from the analysis changed results insofar that the interaction of frontal asymmetry and visual field no longer yielded significance, calling into question the robustness of that finding.

4. Discussion

The present study investigated the role of functional hemispheric asymmetries in both perceptual and inhibitory processes. Importantly, we used the natural variation in hemispheric asymmetry provided by handedness to investigate the lateralized processes that support

Table 4
Regression table for N2 amplitudes –fixed and random effects.

	b	SE	t (df)	p	η^2
Intercept	-4.24	0.23	-18.18 (99)	< 0.001***	0.769
Frontal Asymmetry	0.05	0.48	0.11 (99)	0.91	0.000
Handedness	-0.04	0.23	-0.17 (99)	0.87	0.000
Valence	-0.08	0.03	-2.32 (594)	< 0.05*	0.009
Visual Field	0.08	0.11	0.70 (99)	0.49	0.005
Condition	0.02	0.03	0.45 (594)	0.65	0.000
Valence*Visual Field	-0.03	0.03	-0.78 (594)	0.43	0.001
Valence*Condition	-0.02	0.03	-0.63 (594)	0.53	0.001
Visual Field*Condition	0.07	0.03	2.02 (594)	0.04	0.007
Frontal Asymmetry*Handedness	-0.57	0.48	-0.12 (99)	0.91	0.000
Frontal Asymmetry*Condition†	-0.14	0.07	-2.07 (594)	< 0.05*	0.007
Frontal Asymmetry*Valence*Condition†	-0.02	0.07	-0.36 (594)	0.72	0.000
Frontal Asymmetry*Valence†	0.09	0.07	1.27 (594)	0.21	0.003
Frontal Asymmetry*Visual Field†	0.25	0.23	1.11 (99)	0.27	0.012
Handedness*Visual Field†	0.16	0.11	0.15 (99)	0.88	0.000
Handedness*Valence†	-0.03	0.03	-0.75 (594)	0.45	0.001
Handedness*Condition†	-0.03	0.03	-0.91 (594)	0.36	0.001
Handedness*Visual Field*Condition†	-0.03	0.03	-0.89 (594)	0.37	0.001
Variance Components		Estimate			SE
Residual		0.88			0.05
Intercept		5.22			0.76
Slope Visual Field		1.08			0.17
Cor(Intercept*Slope)		-0.14			0.11

Note. b = regression coefficient; SE = standard error; df = degrees of freedom; η^2 = semi-partial R^2 ; Cor = Correlation; †Cross-level interactions. Df rounded to full number and η^2 to third decimal. All other values rounded to second decimal.

Table 5
Regression table for P3 amplitudes –fixed and random effects.

Parameter	b	SE	t (df)	p	η^2
Intercept	6.00	0.25	24.11 (99)	< 0.001***	0.855
Frontal Asymmetry	-0.03	0.52	-0.06 (99)	0.95	0.000
Handedness	0.11	0.25	0.44 (99)	0.66	0.002
Valence	-0.04	0.05	-0.90 (495)	0.37	0.002
Visual Field	-0.12	0.07	-1.74 (99)	0.09	0.030
Condition	0.72	0.08	8.66 (99)	< 0.001***	0.431
Valence*Visual Field	-0.02	0.05	-0.51 (495)	0.61	0.001
Valence*Condition	-0.04	0.05	-0.87 (495)	0.38	0.002
Visual Field*Condition	-0.07	0.05	-1.51 (495)	0.13	0.005
Frontal Asymmetry*Handedness	-0.19	0.47	-0.40 (99)	0.69	0.002
Frontal Asymmetry*Condition [†]	0.24	0.17	1.39 (99)	0.17	0.019
Frontal Asymmetry*Valence*Condition [†]	0.01	0.10	0.14 (495)	0.89	0.000
Frontal Asymmetry*Valence [†]	0.04	0.10	-0.37 (495)	0.71	0.000
Frontal Asymmetry*Visual Field [†]	-0.29	0.14	-2.11 (495)	< 0.05*	0.043
Handedness*Visual Field [†]	0.00	0.07	-0.03 (99)	0.97	0.000
Handedness*Valence [†]	-0.05	0.05	-1.08 (495)	0.28	0.002
Handedness*Condition [†]	-0.02	0.08	-0.21 (99)	0.83	0.000
Handedness*Visual Field*Condition [†]	0.02	0.05	0.49 (495)	0.63	0.000

Variance Components	Estimate	SE
Residual	1.72	0.11
Intercept	5.85	0.87
Slope Visual Field	0.22	0.06
Slope Valence	0.46	0.10
Cor(Intercept*Slope Visual Field)	-0.28	0.14
Cor(Intercept*Slope_Valence)	0.45	0.11
Cor(Slope Visual Field*Slope Valence)	-0.13	0.17

Note. b = regression coefficient; SE = standard error; df = degrees of freedom; η^2 = semi-partial R²; Cor = Correlation; [†]Cross-level interactions. Df rounded to full number and η^2 to third decimal. All other values rounded to second decimal.

effective response inhibition in the context of emotional stimuli. We also recorded resting-state EEG asymmetry in frontal cortex as a marker of individual differences in prefrontal networks associated with inhibitory control.

As hypothesized, results regarding the N170 confirmed effective stimulus lateralization, with more negative amplitudes over the right hemisphere after stimulus presentation in the LVF, and more negative amplitudes over the left hemisphere after stimulus presentation in the RVF. In accordance with our expectations, we also found evidence for differential lateralization of face processing in left- and right-handers. The interaction of handedness and electrode showed that (across both visual fields) the N170 was more negative over the right hemisphere for right-handers, and more negative over the left hemisphere for left-handers. This indicates left-hemispheric dominance for face processing in left-handers and right-hemispheric dominance in right-handers, which is in line with existing literature (Badzakova-Trajkov et al., 2010; Willems et al., 2010).

It has to be noted that the appropriate sites for scoring the N170 have been a matter of debate (e.g.; Bentin et al., 2007; Rossion & Jacques, 2008). Bentin et al. (2007) emphasized that the N170 is circumscribed around occipito-temporal sites and declines rapidly at more medial and superior sites, possibly even being absent at medial occipital sites. Along these lines, differential effects of stimulus characteristics on N170 amplitudes might not only be most pronounced occipito-temporally, they could also differ when scoring the N170 at other electrodes. In the present study, scalp topographies strongly supported the use of CP5 and CP6 for N170 quantification rather than more posterior and lateral sites (see Fig. 2).

Importantly, as predicted, differential lateralization of early face processing influenced inhibitory task performance. Self-reported right-handers showed fewer false alarms after initial processing in their dominant right-hemisphere; Self-reported left-handers, however, lacked such a lateral advantage, with no difference in inhibitory performance after initial processing in the left or right hemisphere. Often, left-handers show less clear hand dominance in comparison to right-handers

(Dassonville, Zhu, Uurbil, Kim, & Ashe, 1997; Klöppel et al., 2007), creating a confound of handedness direction (i.e., left or right) and the degree of hand preference (i.e., from a clear hand preference to mixed-handedness). Since the exclusion of mixed-handers from analysis did not alter this pattern of the results, it can be assumed that the differences between right- and left-handers were due to direction of handedness and not caused by differences in the degree of hand preference.

Interestingly, the effect of early processing laterality on inhibitory performance was not only modulated by handedness, but also by stimulus valence. As indexed by false alarm rates, the response to angry faces was inhibited more effectively when the face was first processed by the right hemisphere, while the response to friendly faces was inhibited more effectively when the face was first processed by the left hemisphere. Following our line of reasoning, that the response to stimuli is better inhibited after initial processing in the dominant hemisphere, this finding suggests a right-sided dominance for early processing of negative facial expressions, and a left-sided dominance for early processing of positive facial expressions. This is in line with results yielded by other studies using tachistoscopic presentation of faces with different emotional expressions (e.g. Burton & Levy, 1989; Davidson, Mednick, Moss, Saron, & Schaffer, 1987; Reuter-Lorenz, Givis, & Moscovitch, 1983; Wager, Phan, Liberzon, & Taylor, 2003).

Even though laterality effects on response inhibition were found on the behavioural level, results regarding the N2 as an electrophysiological index of response inhibition were not supportive since we failed to observe a more negative N2 in Nogo- versus Go-trials. Given the differential findings obtained for false alarms, it seems unlikely that our experiment failed to elicit and tax neuronal inhibitory control mechanisms. Nevertheless, the (unexpected) lack of a condition (Go vs. Nogo) effect on N2 amplitudes warrants an explanation. Interestingly, a recent study by Adelhöfer, Chmielewski, and Beste (2019) using highly similar Gabor patches as Go and Nogo stimuli also did not observe a Nogo-N2. One reason for not observing a Nogo-N2 could be that this ERP-component might not reflect the operation of an inhibitory processes per se (specifically response inhibition), but rather response

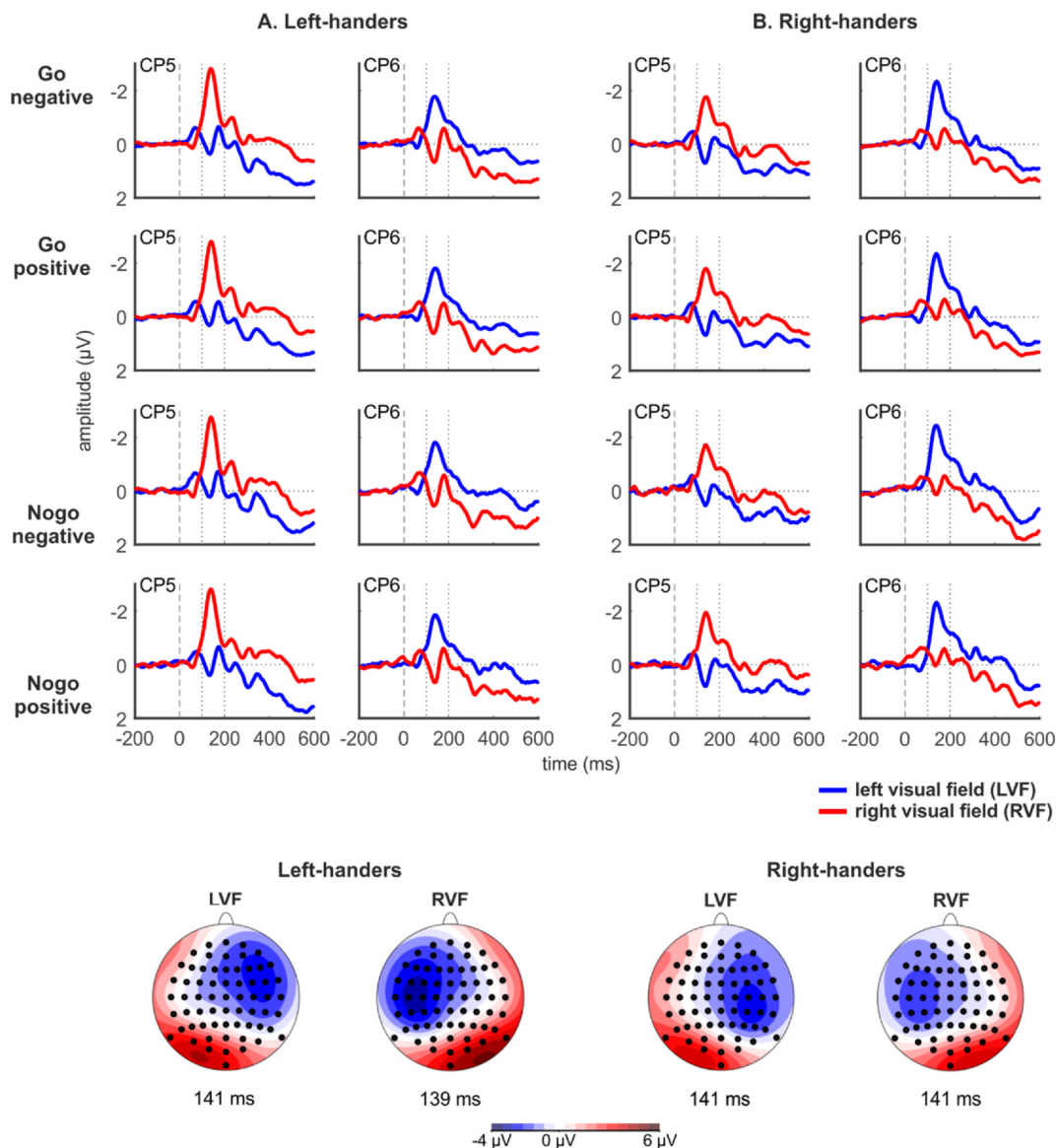


Fig. 2. Grand-average ERPs at electrodes CP5 and CP6 time-locked to stimulus presentation according to condition (Go, Nogo), visual field (LVF, RVF), and valence (positive, negative) in left-handers (A) and right-handers (B). Topographical plots show the scalp distribution at the time point of peak negativity in the N170 time window collapsed across condition and valence.

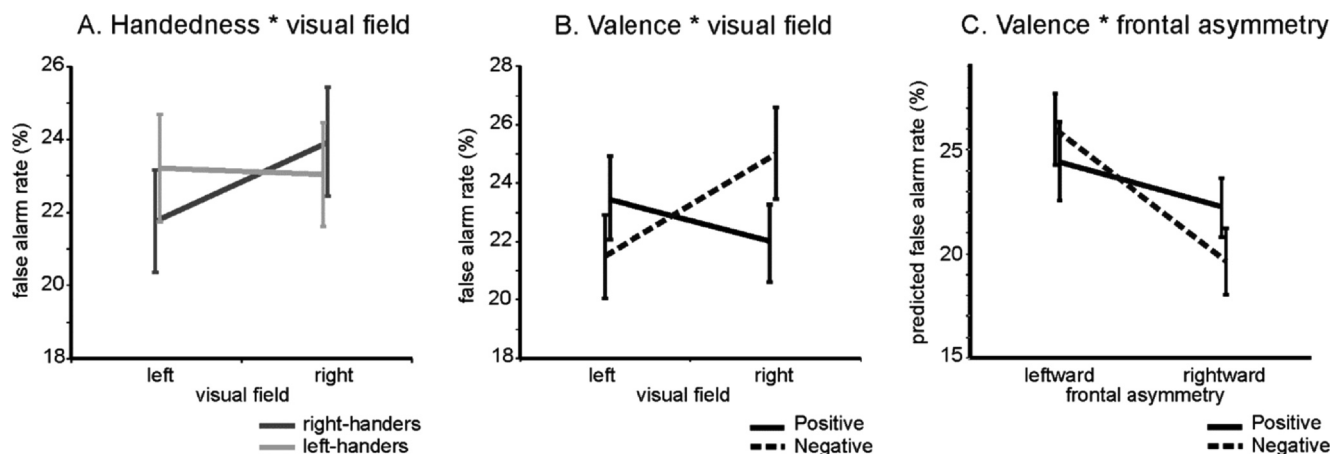


Fig. 3. Mean false alarm rates according to (A) visual field (left/right) for left-handers (LH) and right-handers (RH), (B) visual field and valence (positive/negative), and (C) valence and frontal asymmetry (leftward/rightward). Error bars represent standard errors (SEs).

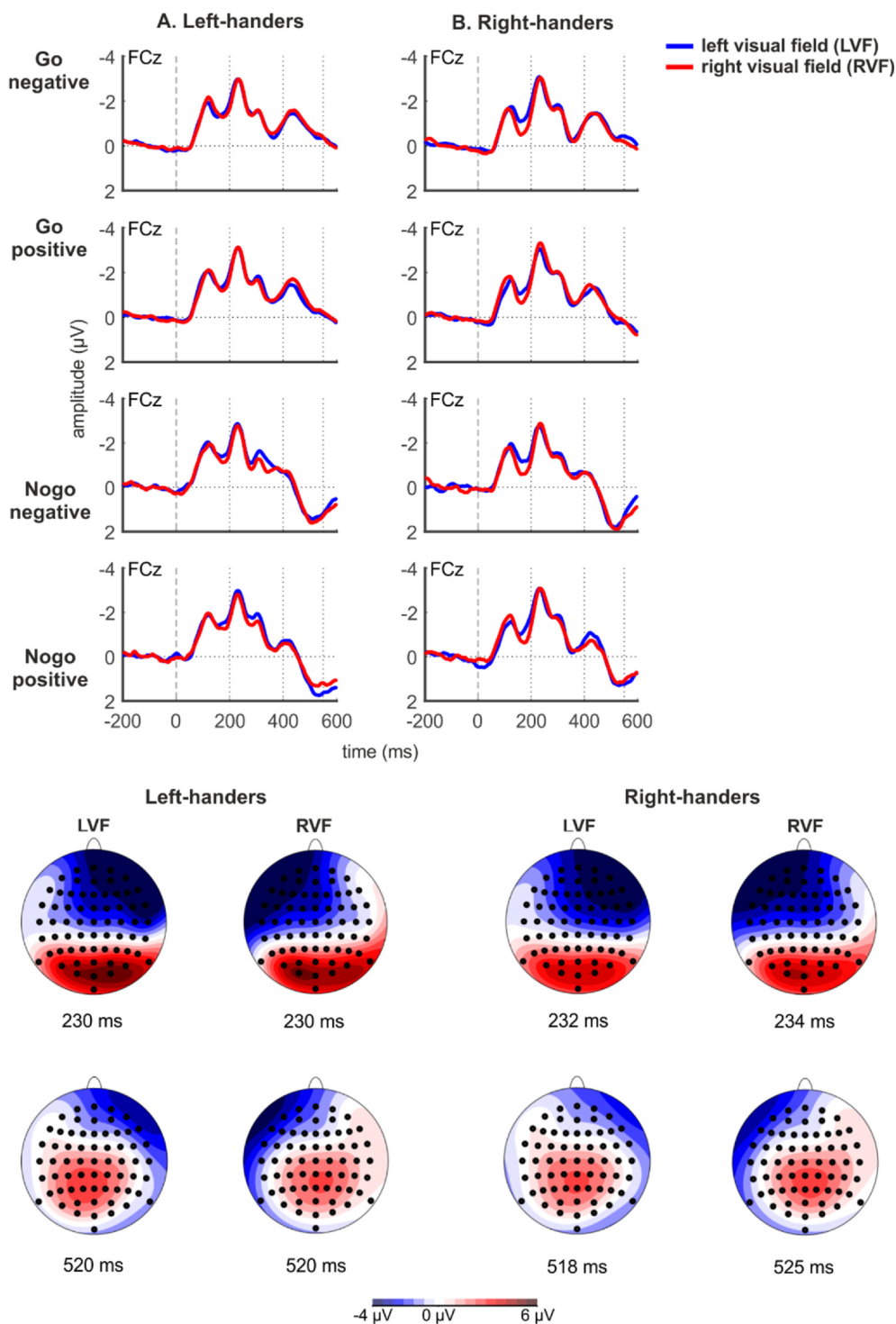


Fig. 4. Grand-average ERPs at electrode FCz time-locked to stimulus presentation according to condition (Go, Nogo), visual field (LVF, RVF), and valence (positive, negative) in left-handers (A) and right-handers (B). Topographical plots show the scalp distribution at the time point of peak negativity in the N2 time window (top) and the time point of peak positivity in the P3 time window (bottom) collapsed across condition and valence.

conflict (Donkers & van Boxtel, 2004; Jones et al., 2002; Nieuwenhuis, Yeung, van den Wildenberg, & Ridderinkhof, 2003b). Response conflict varies as a function of trial frequency. In situations in which a certain response is demanded most of the time (e.g., 80% Go-trial frequency), response conflict is particularly high in those less frequently occurring trials in which another response (e.g., a non-response in the 20% Nogo-trials) is demanded. Nieuwenhuis et al. (2003a) showed that a more negative N2 was obtained for Go-trials in contrast to Nogo-trials when Go-trials were less frequent than Nogo-trials. These findings strongly

support the claim that the pronounced N2 often found for Nogo-trials is not due to response inhibition demand, but because Nogo-trials are less frequent and thus induce higher response conflict. Along these lines, it might be conceivable that our paradigm did not induce enough response conflict to trigger a pronounced Nogo-N2. With 30% occurrence, Nogo-trials were the less frequent trial type in our experiment; however, anecdotally, participants reported that they were not aware of the fact that one of the faces occurred more often than the other within one block. The comparably high miss rates across the experiment (13.2%

versus 8.43% in (Ocklenburg et al., 2013), and even lower in other Go/Nogo-studies, e.g., Voegler et al., 2018) supports this impression (note that one participant whose performance was at chance level was already excluded).

We did observe a P3 that was more positive in Nogo- versus Go-trials; however, none of our expected interactions (nor effects of any other predictors) were observed. A methodological difficulty in interpreting the Nogo-P3 as a cognitive component is its temporal overlap with motor behaviour (Smith, Johnstone, & Barry, 2008). While there is a motor action in all of the Go-trials (traditionally a button press), there is none in the Nogo-trials. Differences regarding the P3 in Nogo- versus Go-trials could therefore be due to movement-related differences rather than inhibition (Nakata et al., 2004). This is specifically relevant for the P3, since its occurrence lies roughly in the same time window as average reaction times. Studies using non-motor responses, such as covert counting, have produced ambiguous results – in some cases, the Nogo-P3 was still observed (Pfefferbaum et al., 1985; Starr, Sandroni, & Michalewski, 1995), in others it vanished or was significantly smaller when no motor response was involved (Bruin & Wijers, 2002; Nakata et al., 2004). If P3 effects in our study are indeed driven by motor rather than cognitive processes, it appears rather plausible that none of the predictors and interactions regarding inhibitory processes had an effect. In future research, non-motor Go/Nogo-tasks should be used to allow the investigation of the Nogo-P3 and related inhibitory processes independent from motor differences.

Focusing on individual frontal alpha asymmetry as an index of higher level inhibitory control, our results are in favour of the AIM (Grimshaw & Carmel, 2014). Following the premise that lower false alarm rates indicate better inhibitory performance, participants with greater relative right frontal activity (reflected in negative frontal asymmetry scores) were better at inhibiting responses to positive information (i.e., friendly faces) than to negative information (i.e., angry faces). Accordingly, participants with greater relative left frontal activity showed a trend towards the opposite pattern.² These findings are consistent with studies linking mood disorders such as depression to greater right frontal activity/lower left frontal activity, presuming that those disorders are accompanied by a lack of successful inhibition of the response to negative information, a notion that has been supported also by studies using other experimental measures such as priming effects (e.g., Joormann & Gotlib, 2010). Moreover, the connection between greater left frontal activity/lower right frontal activity and impulsivity (Gable, Mechin, Hicks, & Adams, 2015; Neal and Gable, 2016, 2017), sensation seeking (Santesso et al., 2008), and addiction (Mechin, Gable, & Hicks, 2016) can be explained in terms of deficient inhibition of the response to (subjectively perceived) positive information.

In contrast to the behavioural data, the present ERP results unfortunately did not offer clear conclusions for or against the AIM or r-BIS, since we did not observe the expected Nogo-N2 effects as outlined above. In contrast to the predictions based on the r-BIS, we did not observe a main effect of frontal asymmetry on false alarm rates. It must be considered whether our experiment did not capture the inhibitory processes the r-BIS model refers to, since the r-BIS is embedded in the motivational theory, and its inhibitory functioning might rather concern resolving conflicts between and within approach and withdrawal motivation. An interesting observation in this matter is that the Nogo-N2 in past studies has been found to be related to self-reported inhibitory control (Amodio, Master, Yee, & Taylor, 2008), and might be localized to the right hemisphere (Bokura et al., 2001). The fact that we did not observe a Nogo-N2 in combination with the lack of r-BIS effects

²Note that modelling random effects reduces degrees of freedom, since more parameters need to be estimated, which in turn reduces power (Kreft & de Leeuw, 2007). Especially, when in simple slope analysis only one half of the data distribution is taken into account, non-significant findings might be due to a lack of power.

might indicate that both relate to the same cognitive process that was not induced in our paradigm.

Last, the present results showed that frontal asymmetry was not linked to handedness. More specifically, left-handers, right-handers, and mixed-handers did not differ in their frontal asymmetry scores during rest. This is in contrast to a recent study (Ocklenburg et al., 2019) which found that stronger right-handedness was associated with greater right relative to left alpha power (i.e., greater left frontal activity). This finding was based on a larger sample that comprised 171 right- and 64 left-handers. However, somewhat similar to the present results, when grouping subjects dichotomously according to handedness rather than using a continuous scale (i.e., the LQ based on the EHI), a direct (post-hoc) comparison of alpha band asymmetry in right- and left-handers also failed to reach significance. More research appears to be needed to clarify the relationship between handedness, the strength of handedness preferences, and frontal asymmetry. Moreover, resting state frontal alpha asymmetry is not free from influences of state variables, which potentially submerge trait-like connections (Harmon-Jones & Gable, 2018) and should thus be taken into account in future studies.

5. Conclusion

The present findings make a strong claim for the proposed dependency of executive functions on early lateralized processes. They confirm theories of differential lateralisation of early face processing in right- and left-handers, and extend the existing literature by showing that those natural hemispheric differences influence the higher cognitive process of response inhibition on a behavioural level. Moreover, our study postulates that response inhibition is not only influenced by early lateralised processing, but also depends on hemispheric differences at a later stage, as indexed by frontal alpha asymmetry. Specifically, the present results suggest that the link between frontal asymmetry and response inhibition depends on emotional valence of the stimulus material, thus offering additional insight into how emotion regulation in the brain might work.

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CRedit authorship contribution statement

Elisabeth Schrammen: Writing - original draft, Formal analysis. **Gina M. Grimshaw:** Writing - review & editing, Conceptualization, Methodology. **Adam Berlijn:** Writing - review & editing, Formal analysis. **Sebastian Ocklenburg:** Writing - review & editing, Conceptualization, Methodology, Project administration. **Jutta Peterburs:** Writing - review & editing, Visualization, Conceptualization, Methodology, Supervision, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://>

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