

Individual Differences in Asymmetric Resting-State Frontal Cortical Activity Modulate ERPs and Performance in a Global-Local Attention Task

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Abstract. Recent research has demonstrated that individual differences in approach motivation modulate attentional scope. In turn, approach and inhibition have been related to different neural systems that are associated with asymmetries in relative frontal activity (RFA). Here, we investigated whether such individual differences in asymmetric hemispheric activity during rest, and self-report measures of approach motivation (as measured by the behavioral inhibition system, BIS/behavioral activation system, BAS scales) would be predictive of the efficiency of attentional processing of global and local visual information, as indexed by event-related potentials (ERPs) and performance measures. In the reported experiment, participants performed a visual attention task in which they were required to either attend to the global shape or the local components of presented stimuli. Electroencephalogram was recorded during task performance and during an initial “resting state” measurement. The results showed that only the BAS-Reward Responsiveness subscale was associated with left RFA during rest, while BIS, BAS-Drive, and BAS-Fun Seeking were associated with more right-lateralized RFA. Importantly, left RFA during the “resting state” measurement was associated with increased P3 (right-lateralized) amplitudes and decreased P3 latencies on trials requiring a global focus. In turn, these ERPs were associated with enhanced performance on trials requiring a global focus. These results provide the first evidence for a positive association between left RFA during rest and increased efficiency of right-lateralized brain mechanisms that are involved in processing global information.

Keywords: attention, focus, alpha power, alpha asymmetry, lateralization, qEEG

The question whether perception is an analytic or holistic process has been under debate for a long time (see Kimchi, 1992, for a review). Whereas proponents of structuralism argued that the basic elements of perception were independent local components and the eventual perception of organized wholes could only be achieved through associative learning (e.g., Wundt, 1874), Gestaltists (e.g., Wertheimer, 1967) argued that people perceived the world in patterns and wholes and that the perception of these organized units is not the mere result of associative learning but instead, an immediate product of brain processes in response to the entire visual object. Navon (1977) was one of the first to

experimentally test whether perception of visual stimuli occurs in a more piecemeal fashion or whether objects are instantaneously perceived as a whole. In several experiments, Navon discovered that the perceptual process is temporarily organized in such a way that initial global structuring gradually proceeds toward a more specific focus on local parts of a given stimulus. Moreover, he found that local features of a stimulus did not interfere with recognition of its global structure, whereas recognition of the local constituents was affected by the global features of the same stimulus. These results implied that while it is possible to attend to a stimulus without processing its local constituents,

the global structure cannot be ignored when attending to the local attributes. Navon (1977) coined this phenomenon the “global precedence effect.”

Although in general people first perceive the global shape of an object before processing the local constituent parts in more detail, recent research has demonstrated that individual differences in approach/avoidance motivation or related positive/negative affect (e.g., Carver, Sutton, & Scheier, 2000) modulate perceptual scope (Derryberry & Tucker, 1994; Friedman & Förster, 2010). For example, Gasper and Clore (2002) showed that participants in sad moods were less likely to rely on global information than those in happier moods. Similarly, Basso, Scheffé, Ris, and Dember (1996) found that trait happiness (an affective concomitant of approach motivation; Carver et al., 2000) was associated with the inclination to perceive figures according to their global as opposed to their local structure. In addition, Förster, Friedman, Özelsel, and Denzel (2006) illustrated that manipulated approach or avoidance motivation led to opposite effects on attentional scope. These authors manipulated motivational orientation by making participants complete a maze by either leading a mouse to the exit, where it would find cheese (approach), or they had to find the exit of the maze to let the mouse escape from a depicted owl hovering above the maze (avoidance). This manipulation has been validated to induce either an approach or an avoidance motivational state (Friedman & Förster, 2005). Indeed, participants in the approach condition demonstrated faster response times to global targets, whereas responses for those in the avoidance condition were faster to local targets.

Perspectives on approach and inhibition behavior have been shaped to a large extent by the theory postulated by Gray (1987) that proposes two interacting motivational systems: the behavioral inhibition system (BIS) and the behavioral activation system (BAS). According to Gray, the BIS is sensitive to signals of punishment and inhibits behavior that may lead to aversive or harmful outcomes. In contrast, the BAS is sensitive to positive signals of reward. In the psychophysiological literature, approach and inhibition have been related to different neural systems that are associated with “resting state” asymmetries in frontal cortical activity (relative frontal activity, RFA) as measured using electroencephalography (EEG; see Coan & Allen, 2003, for a review). Approach, a promotion focus, approach-related positive affect, and a social context stimulating approach, have all been related to greater left-sided RFA (Amodio, Master, Yee, & Taylor, 2004; Amodio, Shah, Sigelman, Brazy, & Harmon-Jones, 2008; Boksem, Smolders, & De Cremer, in press; Sutton & Davidson, 1997; Tomarken, Davidson, Wheeler, & Kinney, 1992), while behavioral inhibition, avoidance-related negative affect, and a prevention focus have been associated with greater right-sided RFA (Amodio et al., 2004; Coan & Allen, 2003; Henriques & Davidson, 1990; Shackman, McMenamin, Maxwell, Greischar, & Davidson, 2009). RFA measures have been shown to be highly reliable over time; Tomarken and colleagues (1992) showed that individual differences in baseline RFA are stable over a period of weeks and exhibit excellent internal consistency and reliability, suggesting that these measures index a trait-like construct. Together, these

findings suggest that approach and left RFA should be associated with a global attentional focus, while avoidance/inhibition and right RFA should be related to a local focus.

However, findings in the literature have not always been consistent. Although the studies mentioned so far showed a positive relation between positive affect/approach motivation (associated with left RFA) and a global focus, while negative affect/avoidance motivation (associated with right RFA) was shown to be related to a more local focus, Gable and Harmon-Jones (2008) have reported contradictory results. In their study, responses to global stimuli were not faster but slower after pictures that should induce approach-motivated positive affect (desserts) than after neutral pictures (rocks), whereas the reverse was found for responses to local stimuli, which were faster after dessert pictures than after rock pictures. These findings are difficult to reconcile with, for example, the study by Förster et al. (2006), who illustrated that manipulated approach motivation increased attentional scope, while avoidance motivation reduced it.

What is more, Harmon-Jones and Gable (2009) unexpectedly found that greater left RFA recorded during the presentation of pictures inducing approach-motivated positive affect predicted faster reactions to local targets. Hence, these authors concluded that approach-motivated positive affect and left RFA do not lead to broadening but instead to a narrowing of attentional scope.

Although the findings of Harmon-Jones and Gable appear to fit with the widely accepted idea that the right hemisphere is more involved in global attention, while the left hemisphere is involved in local, focused attention (e.g., Van Kleeck, 1989), this is not so straightforward: While approach motivation and affect are related to asymmetrical *frontal* activity (as suggested by the term “relative frontal activation”; e.g., Sutton & Davidson, 1997), differences in local and global attentional focus are related to asymmetrical *central/parietal* activity (e.g., Derryberry & Reed, 1998; Fink et al., 1996; Volberg & Hubner, 2004; Volberg, Kliegl, Hansimayr, & Greenlee, 2009). Thus, effects on asymmetrical brain activity differ and may even reverse for frontal and posterior brain areas. Indeed, affective states characterized by both arousal and positive valence have been proposed to be associated with greater left than right frontal activity, but also with enhanced right-posterior (parietotemporal) activity (Heller, 1993).

Another thing that may have led to confusion is that relations between RFA and motivation/affect have been found with “resting state” RFA (i.e., EEG activity measured while subjects have their eyes closed and do nothing; e.g., Coan & Allen, 2003), which has been argued to reflect a trait measure of motivational orientation and dispositional affect (Sutton & Davidson, 1997; Tomarken et al., 1992), while lateralizations associated with global/local processing have been observed during task performance.

To reconcile these divergent findings it would be beneficial to measure both “resting state” RFA, as well as brain activity during a global/local attention task, and relate these measurements to individual differences in motivational orientation (BIS/BAS). This would enable us to dissociate baseline asymmetrical brain activation, perhaps reflecting a dispositional motivational orientation, from asymmetrical activation associated with the actual focusing (global or

local) of attention. This is what we set out to do in the present study.

Event-related potentials (ERPs) have been used extensively to investigate the processing of global and local information and the proposed associated hemispheric asymmetries (e.g., Heinze & Münte, 1993; Heinze, Johannes, Münte, & Mangun, 1994; Malinowski, Hubner, Keil, & Gruber, 2002; Proverbio, Minniti, & Zani, 1998; Yamaguchi, Yamaguchi, & Kobayashi, 2000). The most consistent findings include enhanced early visual attention components (P1 and N1; 100–200 ms post-stimulus onset) and an increase in a late positivity in the P3 latency range (300–500 ms) when stimuli require a global attentional focus. Recorded over lateral occipital sites, these early visual components have been proposed to reflect a “sensory gain mechanism” (Hillyard, Mangun, Luck, & Heinze, 1990; Luck, Heinze, Mangun, & Hillyard, 1990; Vogel & Luck, 2000): As a result of top-down visual attention, the responsivity of extrastriate visual cortex to stimuli presented at attended locations is amplified, enhancing further processing of these stimuli. Also the P3 component is thought to reflect attentional mechanisms (e.g., Herrmann & Knight, 2001; Polich, 2007). The P3 is modulated by the amount of attention allocated to the stimulus (Herrmann & Knight, 2001; Kok, 2001; Nieuwenhuis, Aston-Jones, & Cohen, 2005) and is thought to reflect stimulus classification specifically (Donchin & Coles, 1988; Duncan-Johnson, 1981). Differences in ERP amplitudes are usually interpreted as measures of differences in activity of underlying neural generators. Therefore, differences in involvement of left and right hemispheres in local and global attentional processing, respectively, may be reflected by lateralization of ERP components. Indeed, there have been reports that both early visual components and later P3 amplitudes may be right-lateralized for global stimuli, while they are left-lateralized for local stimuli (e.g., Han, Fan, Chen, & Zhou, 1997; Proverbio et al., 1998), although other studies did not find such lateralization effects (e.g., Heinze, Hinrichs, Scholz, Burchert, & Mangun, 1998).

In the present study, participants performed a Navon task with identical probabilities for global and local stimuli. Stimuli consisted of large capital letters that were composed of either small identical or different letters, and participants were required to either attend to the global shape (large letter) or the local components (small letters) of the stimulus. EEG was recorded during task performance and during an initial “resting state” measurement.

If the scope of perceptual focus is indeed influenced by baseline RFA, individuals with relative left frontal activation (associated with approach motivation) should be better at global processing than local processing and should display larger P3 and early visual component amplitudes with shorter latencies for global stimuli than for locally attended stimuli. In addition, these ERP effects may show a right lateralization at posterior scalp positions, indicating enhanced efficiency of right-lateralized brain mechanisms involved in processing global information in subjects with relative left “resting state” frontal cortical activation. Predictions for individuals with relative right frontal activation (associated with inhibition/avoidance) are somewhat more complex, due to the global precedence effect (Navon, 1977). Still,

individuals with relative right RFA and a more narrow attentional focus should be better at processing the local components of a stimulus than individuals with a broader focus, which should result in a smaller difference in P3 amplitude and latency between local and global stimuli for those with right RFA. Moreover, right lateralization of ERP components elicited by a global attentional focus may be less pronounced for these subjects.

Methods

Participants

Twenty-seven students of Tilburg University (5 males; mean age = 21.7, $SD = 4.9$) participated in exchange for extra course credit. They were paid for their participation and had normal or corrected-to-normal vision. Written informed consent was obtained prior to the study.

BIS/BAS-Scale

Gray (1987) proposed that two general motivational systems underlie behavior and affect: BIS and BAS. We used the Dutch version (Franken, Muris, & Rassin, 2005) of the 24-item BIS/BAS-scale created by Carver and White (1994) to assess dispositional BIS and BAS sensitivities. The BAS dimension contains the following subscales: BAS-Reward responsiveness (BAS-Reward), BAS-Drive (BAS-Drive), and BAS-Fun Seeking (BAS-Fun Seeking). The BIS has no subscales.

Task

The experimental task involved a version of the Navon task (Navon, 1977) in which participants were to identify either the global structure or local parts of the stimulus, which was either a capital letter “S” or “H,” composed of small “S”s or “H”s. Stimuli could be either congruent (e.g., a large “H” composed of small “H”s) or incongruent (e.g., a large “S” made of smaller “H”s). In total, 360 trials were presented to the participant with an equal occurrence of congruent and incongruent stimuli and an equal number of stimuli that required a global or a local focus.

Indicated by a pre-stimulus cue, participants had to focus on the global shape (large letter) or the local units (small letters) of the stimulus. If the target letter was an “H,” participants had to respond by pressing the button under their left index finger; when the target letter was an “S” participants had to press the button under their right index finger. On each trial, a fixation cross was displayed in the middle of the screen and after 1,000 ms the cue “global” or “local” appeared above this fixation mark to indicate the stimulus attribute participants had to focus on. After 1,250 ms, both fixation cross and cue disappeared and immediately thereafter, the stimulus was displayed in the center of the screen for another 1,250 ms. Responses between 100 and 1,250 ms

after stimulus presentation were registered as hits. Following a 500 ms fixation interval, feedback was displayed above the fixation cross; for correct responses, the word “correct” appeared in green whereas for incorrect responses the word “incorrect” would appear in red.

Procedure

Participants were first instructed to complete a practice session (100 trials) to get used to the experimental task they would later engage in. After this, they filled out the BIS/BAS questionnaire and the electrodes were applied. Following the application of the electrodes, subjects were seated in a dimly lit, sound-attenuated, electrically shielded room at 1.20 m from a 17" PC monitor. An EEG resting-state measurement was obtained from all participants to measure baseline (asymmetrical) brain activity. During this measurement, participants were required to close their eyes, sit still, and do nothing for 3 min. Finally, subjects performed 360 trials of the experimental task while EEG was recorded. Their index fingers rested on response buttons which they were instructed to press as quickly as possible when a target was presented, maintaining a high level of accuracy. Upon completion, subjects were debriefed and paid.

Psychophysiological Recording and Analysis

EEG was recorded from 48 sites using active Ag-AgCl electrodes (Biosemi ActiveTwo, Amsterdam, the Netherlands) mounted in an elastic cap. Horizontal EOGs were recorded from two electrodes placed at the external canthi of both eyes. Vertical EOGs were recorded from the infra- and supraorbit of the left eye. EEG and EOG signals were sampled at a rate of 256 Hz, and offline referenced to an averaged mastoid reference. All EEG analyses were performed using the Brain Vision Analyzer software (Brain Products GmbH, Munich, Germany, <http://www.brainproducts.com>). The data were resampled at 100 Hz and further filtered with a 0.53 Hz high-pass filter and a 40 Hz low-pass filter both with a slope of 48 dB/oct. Artifacts were rejected and eye movement artifacts were corrected (Gratton, Coles, & Donchin, 1983).

Electroencephalography

The time period in which the resting-state measurement was recorded, was segmented in 50% overlapping, 5.12 s segments. The data were submitted to a fast Fourier transform (FFT), using a 100% Hanning window. Complete attenuation of the jump discontinuity effect caused by performing FFT on segmented EEG data was realized by using this window, while a 50% overlap ensures that data at the edge of one segment (where it is dampened the full 100%) are not attenuated in the next segment, which results in a minimum of data loss due to this attenuation near the edges of the segments. To normalize the distributions, average segments were log-transformed.

Averaged spectral power within the alpha frequency range was calculated for every electrode because alpha

power (activity in the 8–12 Hz frequency range) is inversely related to cortical activity (Laufs et al., 2003). To obtain a measure of left-right asymmetrical brain activity, asymmetry scores were calculated for fronto-central and centro-parietal electrode pairs (FC6-FC5 and CP6-CP5) by subtracting the spectral power value for the left side from the right side for each pair; in this way it was also possible to control for individual differences such as skull thickness (e.g., Tomarken et al., 1992). Positive asymmetry scores for alpha power reflect greater left-sided neural activity. In addition to this “resting state” measurement of asymmetrical brain activity, we created a similar measure for asymmetrical activations during task processing, following the exact same procedure.

Event Related Potentials

A baseline voltage over the 100 ms interval preceding stimulus onset was subtracted from the waveforms. The ERPs were averaged over replications and calculated separately for each subject, and stimulus category. Using the grand average waveforms, we determined the electrodes showing the largest amplitudes for each of the ERP deflections of interest (P1, N1, and P3). The P1 and N1 were maximal at O1 and O2 and were quantified as the average amplitude in the 80–120 ms and 120–180 ms latency intervals, respectively. P3 amplitude was maximal at Pz and was quantified as the average amplitude in the 300–500 ms time interval.

Statistical Analyses

To investigate the relationships between the BIS/BAS measures and asymmetrical brain activation, we entered scores on the BIS/BAS-(sub)scales in a linear regression model to predict asymmetrical brain activity, both as measured during rest as well as during task-performance. The main benefit of this approach (above calculating correlations) is that it enables us to show relationships between particular BIS/BAS subscales and RFA, while controlling for relationships between RFA and the other subscales, thus revealing the unique contribution of that subscale to RFA.

To investigate the impact of individual differences in RFA on the speed and accuracy of processing global and local information, a 2 (global vs. local focus) \times 2 (congruent vs. incongruent stimuli) repeated-measures general linear model (GLM) with RFA as a covariate was conducted on both reaction times (RTs) and accuracy measures. A similar GLM was used for analyses of ERP amplitude and latency data.

Results

Individual Differences and Asymmetrical Brain Activity

Table 1 shows that, while BAS-subscales were positively correlated, BIS was negatively correlated with BAS-Fun

Table 1. Correlations between BIS and BAS (sub)scales

	BIS	BAS-Drive	BAS-Reward	BAS-Fun Seeking
BIS		-.22	.25	-.14
BAS-Drive	-.22		.44*	.24
BAS-Reward	.25	.44*		.28
BAS-Fun Seeking	-.14	.24	.28	

Notes. $N = 28$; * $p < .05$.

Seeking and BAS-Drive, but was positively correlated with BAS-Reward. These findings are comparable to what we have previously found in a larger population of subjects ($N = 88$; Tops & Boksem, 2010). As shown in Table 2, only BAS-Reward predicted larger left RFA during rest, while BIS and the other BAS-subscales predicted larger right RFA. These effects were not observed at posterior sites (Table 3); indeed, BIS even predicted more left-sided posterior activity as measured during rest. In contrast, when we look at asymmetrical activations during task performance

Table 2. Regression analysis with Rest-RFA as dependent variable

	t	β	p
Dependent: Rest-RFA			
BIS	-2.12	-.41	.04
BAS-Drive	-2.21	-.46	.03
BAS-Reward	2.75	.57	.01
BAS-Fun Seeking	-2.10	-.40	.04

Notes. $N = 28$. $R^2 = .37$; $F(4, 25) = 3.10$, $p < .05$. RFA = relative frontal activation.

Table 3. Regression analysis with Rest-RPA as dependent variable

	t	β	p
Dependent: Rest-RPA			
BIS	2.19	.41	.04
BAS-Drive	-2.07	-.40	.05
BAS-Reward	0.06	.01	.95
BAS-Fun Seeking	1.65	.30	.11

Notes. $N = 28$. $R^2 = .43$; $F(4, 24) = 3.73$, $p < .05$. RPA = relative posterior activation.

Table 4. Regression analysis with Task-RFA as dependent variable

	t	β	p
Dependent: Task-RFA			
BIS	-1.28	-.29	.21
BAS-Drive	-.42	-.10	.68
BAS-Reward	.11	.03	.91
BAS-Fun Seeking	.96	.21	.35

Notes. $N = 28$. $R^2 = .13$; $F(4, 26) = .81$, ns. RFA = relative frontal activation.

Table 5. Regression analysis with Task-RPA as dependent variable

	t	β	p
Dependent: Task-RPA			
BIS	.69	.14	.50
BAS-Drive	-2.23	-.47	.04
BAS-Reward	1.18	.26	.25
BAS-Fun Seeking	1.09	.22	.29

Notes. $N = 28$. $R^2 = .56$; $F(4, 24) = 2.23$, $p = .10$. RPA = relative posterior activation.

(Tables 4 and 5), we see that BAS-Drive predicted more right relative posterior activity (RPA).

Behavioral Data

Reaction Times

To investigate individual differences in RTs, a 2 (global vs. local focus) \times 2 (congruent vs. incongruent stimuli) repeated-measures ANOVA with RFA as a covariate was conducted. A significant main effect of focus was revealed, $F(1, 26) = 118.40$, $p < .001$; participants responded significantly faster to targets that required a global focus ($M = 530$, $SD = 15$) compared to stimuli that required a local focus ($M = 596$, $SD = 16.20$). Likewise, responses were faster for congruent targets ($M = 547$, $SD = 15$) than for incongruent targets ($M = 579$, $SD = 15$); $F(1, 26) = 84.05$, $p < .001$. Furthermore, an interaction effect was found between Focus (global vs. local) and Congruency (congruent vs. incongruent); participants responded faster on global congruent ($M = 523$, $SD = 81$) and local congruent trials ($M = 570$, $SD = 88$) than on global incongruent ($M = 537$, $SD = 82$) or local incongruent trials ($M = 622$, $SD = 85$), but these differences in RTs between congruent and incongruent trials were significantly larger on trials that required a local focus compared with trials that required a global focus, $F(1, 26) = 36.06$, $p < .001$. These effects on RT were found not to interact with any of the individual differences in BIS/BAS or asymmetrical brain activity.

Response Accuracy

Subsequent analysis of response accuracy showed that the degree of error commission was dependent on asymmetrical posterior activity during task performance (Task-RPA). We

found a Focus \times Task-RPA interaction, $F(1, 23) = 10.22$, $p < .005$, indicating that more right-posterior activity was associated with fewer errors on stimuli requiring a global focus, $r(25) = .56$, $p < .005$, while errors on trials requiring a local focus were unrelated to Task-RPA, $r(25) = .31$, ns. As expected, error percentages were lower for congruent trials (1.6%; $SD = .01$) than for incongruent trials (5.3%; $SD = .01$; $F(1, 23) = 13.64$, $p < .001$). This difference was also influenced by Task-RPA, $F(1, 23) = 6.67$, $p < .05$: While more right Task-RPA was associated with fewer errors on incongruent trials, $r(25) = .51$, $p < .01$, Task-RPA was unrelated to the number of errors committed on congruent trials, $r(25) = .14$, ns. Finally, a significant three-way interaction was found between Focus, Congruency, and Task-RPA, $F(1, 23) = 7.13$, $p < .05$. Focus interacted with Task-RPA on incongruent trials, $F(1, 23) = 10.37$, $p < .005$, but not on congruent trials, $F(1, 23) = .53$, ns. Specifically, the number of errors on incongruent trials requiring a global focus was found to be significantly related to Task-RPA, $r(25) = .57$: Subjects with more right-posterior activity made fewer errors on incongruent global trials. All other correlations were nonsignificant.

Electrophysiological Results

Early Visual Components

While analyses of amplitudes in the 80–120 ms latency range on O1 and O2 (corresponding to the P1 component, see Figure 1) did not show any significant effects, analysis of amplitudes in the 120–180 ms latency range (corresponding to the N1, see Figure 1) revealed that global trials elicited larger amplitudes compared to local trials, $F(1, 24) = 10.72$, $p < .005$, while amplitudes were also slightly larger for incongruent trials, $F(1, 24) = 7.11$, $p < .05$. In addition, we found a three-way interaction between Focus, Congruency, and

Rest-RFA, $F(1, 24) = 4.14$, $p < .05$. Follow-up analyses showed that for incongruent trials, global stimuli elicited a larger N1 than local stimuli, $F(1, 24) = 5.48$, $p < .05$. For congruent trials, however, we observed a Focus \times Rest-RFA interaction, $F(1, 24) = 15.47$, $p < .001$, indicating that this effect of Focus (i.e., a larger N1 for global targets) was only observed for subjects with a right Rest-RFA (see Figures 2 and 3). To quickly summarize these N1 effects, we found that global targets elicited a larger N1 compared to local targets, except for subjects with a left RFA, who did not show this increase in amplitude for global targets when the stimulus was congruent.

P3

A 2 (global vs. local focus) \times 2 (congruent vs. incongruent targets) repeated-measures ANOVA with RFA as a covariate revealed that overall, global trials resulted in more positive P3 (300–500 ms) amplitudes than local trials, $F(1, 24) = 144.04$, $p < .001$ (Figure 1). Likewise, the P3 was more pronounced for congruent than for incongruent stimuli, $F(1, 24) = 35.63$, $p < .001$. More importantly, approach motivation was found to strongly interact with focus, $F(1, 24) = 35.52$, $p < .001$, indicating that the difference in amplitude between global and local trials was most pronounced for subjects with left RFA, $r(27) = -.77$, $p < .001$ (Figures 2 and 3). RFA was not found to interact with congruency, $F(1, 24) = 2.40$, ns.

P3 latencies were also found to differ as a function of attentional focus; a one-way repeated-measures ANOVA with level of focus as the independent factor and RFA as a covariate revealed that latencies were significantly shorter for global trials ($M = 398$, $SD = 9.1$) than for local trials ($M = 430$, $SD = 11.2$; $F(1, 24) = 14.79$, $p < .001$). Although not significantly so, focus tended to interact with RFA, $F(1, 24) = 2.29$, $p = .14$. Further inspection showed

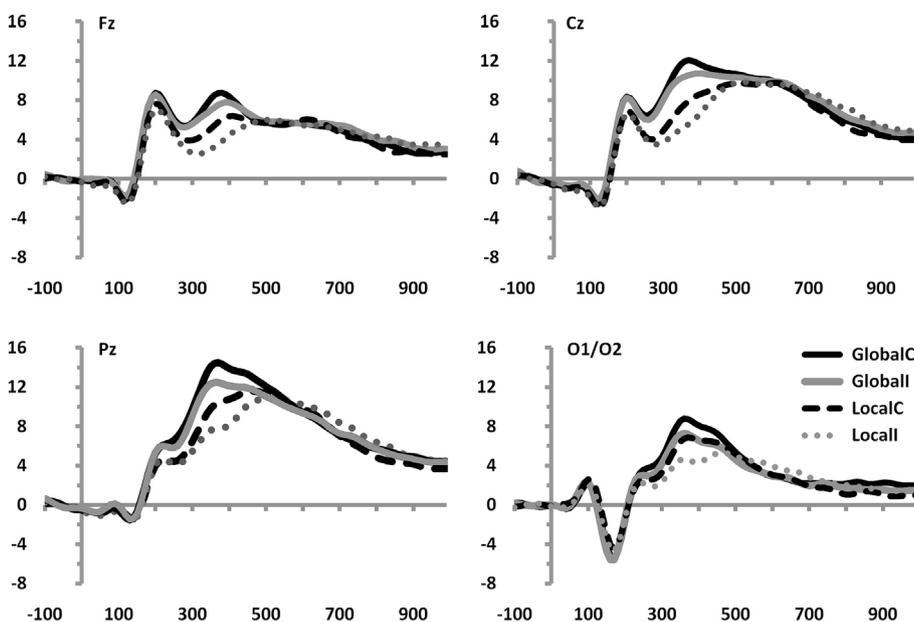


Figure 1. ERPs elicited by the four stimulus conditions (Global, Local, Congruent, and Incongruent) at midline electrode sites.

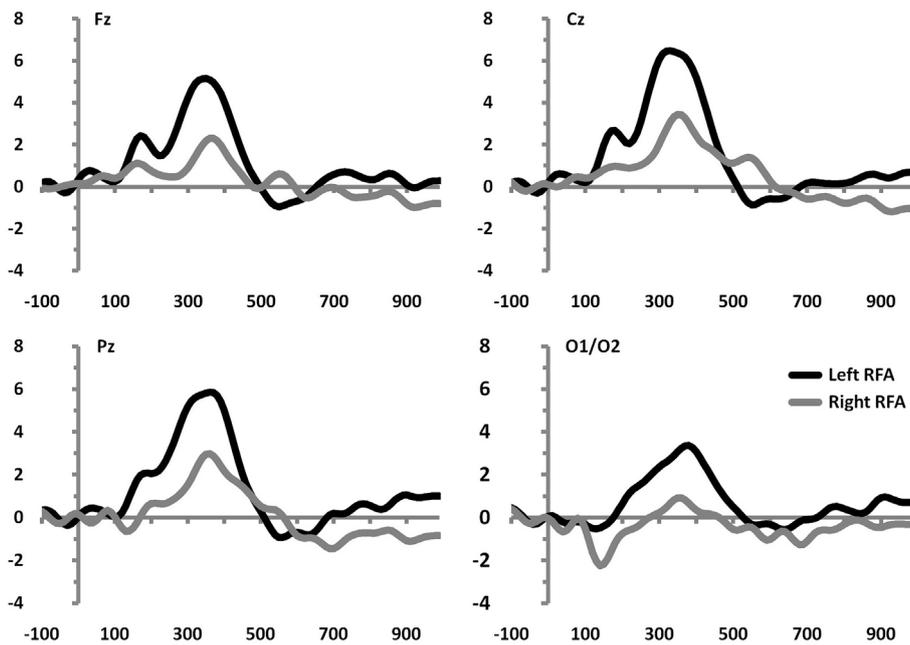


Figure 2. Difference waves, created by subtracting ERPs elicited by trials requiring a local focus from trials requiring a global focus. The black trace represents amplitudes for subjects with a more left RFA, while the gray trace represents amplitudes for subjects with more right RFA. For illustrational purposes only, these groups were created by a median split procedure.

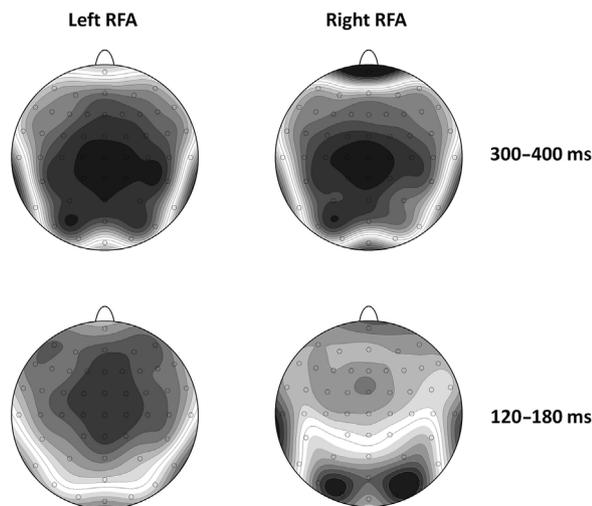


Figure 3. Distribution of activity over the scalp, as reflected by the difference waves in Figure 2, for both early (120–180) and late (300–400) latency intervals. For illustrational purposes only, left and right RFA groups were created by a median split procedure.

that for global stimuli, RFA was significantly associated with P3 latencies, with shorter latencies for those with more left RFA, $r(27) = -.43$, $p < .05$. P3 latencies on local trials were not related to RFA, $r(27) = -.15$, ns.

Although we also found that on Pz, amplitudes of the P2 (160–220 ms) and N2 (220–300 ms) components were significantly more positive for global trials, $F(1, 24) = 7.59$, $p < .05$ and $F(1, 24) = 10.93$, $p < .005$, respectively, this effect was unrelated to RFA, $F(1, 24) < .57$, ns (similar results were obtained from Cz, see Figure 1). In addition,

these effects do not seem to be specific for the different ERP components, but appear to have resulted from a general overlapping slow positivity for global trials. Indeed, topological distribution over the scalp was similar for these three components, suggesting that these amplitudes resulted from activity within the same neural generator (Mangun & Hillyard, 1995). Including the factor Time (160–220, 220–300, 300–500 ms) as a factor in the GLM only shows a significant linear contrast of Time \times Focus, $F(1, 21) = 8.80$, $p < .01$, indicating a linear increase in the difference in amplitude between local and global trials, reaching a maximum in the P3 latency range. Together, this shows that we found no evidence for differential effects of Focus on P2, N2, and P3. Instead, our results suggest that the main difference between global and local trials is a slow positive wave, peaking between 300 and 500 ms over central-parietal areas.

Difference Waves

To investigate the ERP effects of attentional scope further, we computed difference waves by subtracting ERPs elicited by local trials from ERP elicited by global trials (Figure 2). Such a difference-wave approach is useful because peak amplitudes and latencies in the ERP may result from activity of simultaneously active latent neural components, and this activity may only be loosely related to observed amplitudes and latencies in the ERP (Holroyd & Krigolson, 2007; Luck, 2005). Inspecting these difference waves, we see that, in addition to an early effect on occipital electrodes (corresponding to the N1), the most prominent difference between global and local trials is a large deflection peaking between 300 and 400 ms on Cz. This difference appears to be larger for subjects with left RFA and appears to peak earlier and more anterior than the P3. In addition, this deflection seems to be right-lateralized for subjects with left RFA, while it

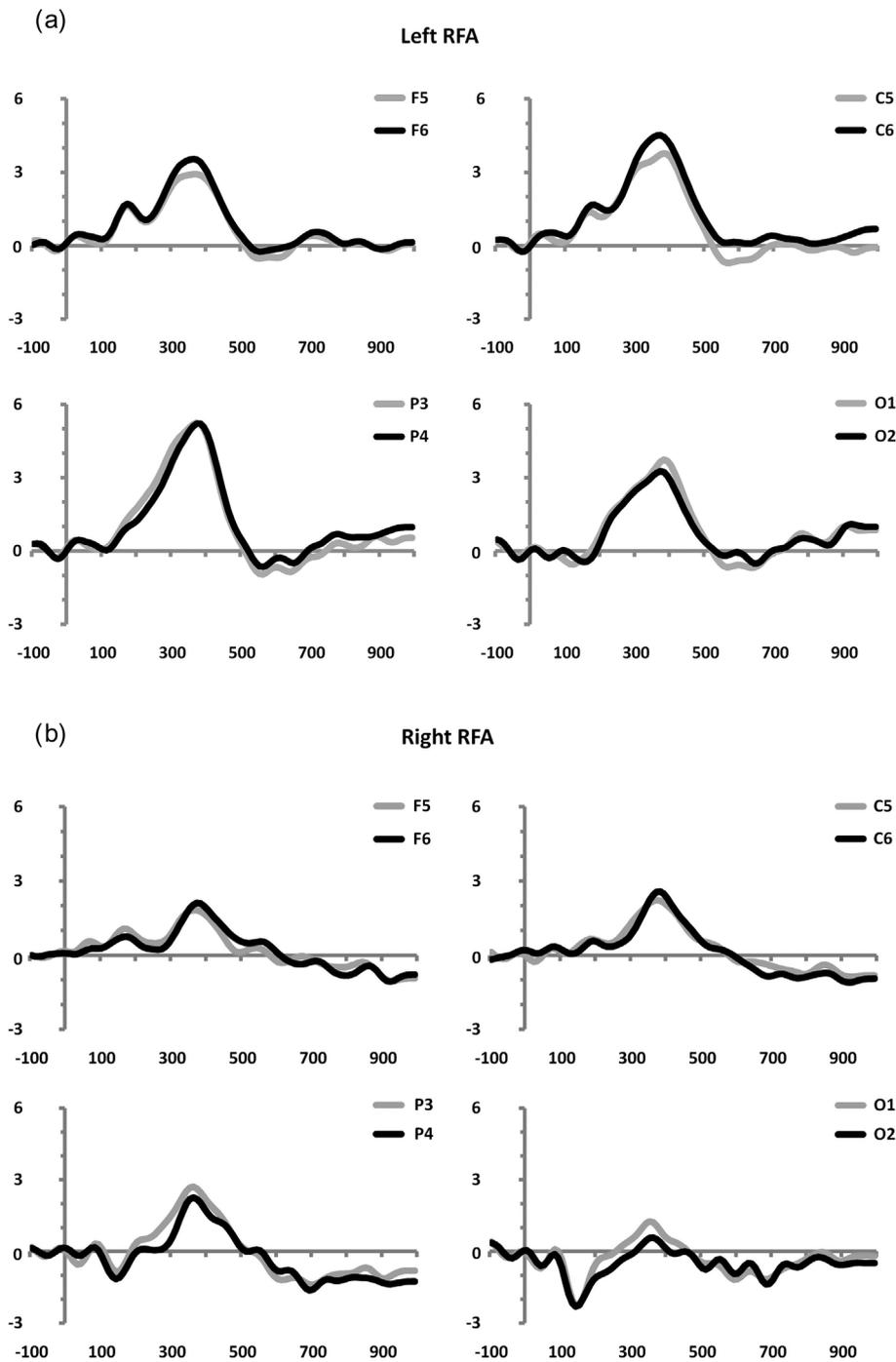


Figure 4. Lateralization of difference-wave amplitudes for (a) subjects with more left RFA and (b) subjects with more right RFA. Amplitudes in the 300–400 ms latency range were shown to be more positive at right central electrode sites (black traces) for subjects with left RFA.

appears to be somewhat left-lateralized for subjects with right RFA (Figure 3). To analyze this effect further, we submitted the amplitude of this difference wave (300–400 ms) at C5, Cz, and C6 to a GLM. The results showed that, in addition to a main effect of RFA, $F(1, 24) = 28.25, p < .001$, indicating a larger deflection for subjects with left RFA, we observed a significant quadratic contrast, $F(1, 24) = 57.56, p < .001$, indicating that amplitudes were most pronounced at Cz, but also a significant interaction of this latter effect with

RFA, $F(1, 24) = 9.96, p < .005$, indicating that this distribution over the scalp differed for subjects with left and right RFA (see Figure 3). Follow-up analysis including only C5 and C6 showed that for left RFA subjects amplitudes were larger over the right hemisphere, while for subjects with right RFA, this effect was substantially less pronounced, $F(1, 24) = 6.72, p < .05$ (see Figure 4). Finally, we found the effect of Focus on the amplitude of the difference wave to be related to RTs, $r(27) = -.50, p < .01$: The larger the

increase in positivity for global trials as compared to local trials, the faster subjects were on trials requiring a global focus.

Discussion

In this study, we investigated whether individual differences in approach motivation and differences in hemispheric activity, both during rest and task performance, would be associated with attentional scope. We expected that approach motivation and associated left “resting state” RFA would be associated with a relatively broad attentional scope, which in turn would be associated with enhanced right-posterior brain activity during task performance.

Our findings however turned out to be somewhat less straightforward. While we predicted that approach motivation (as measured by the BAS) would be associated with left RFA during rest, only the BAS-Reward subscale displayed this pattern of activity. The other BAS-subcales even showed the reverse pattern: Just like BIS, BAS-Drive and BAS-Fun were associated with more right RFA during rest. One possible explanation for this finding could be that the different BAS-subcales reflect different aspects of approach and reward processing. The Drive scale is made of items pertaining to the persistent pursuit of desired goals and the Fun Seeking scale has items reflecting both a desire for new rewards and a willingness to approach a potentially rewarding event on the spur of the moment (Carver & White, 1994). Both subscales seem to reflect the willingness to act in the context of potential rewards (“wanting”), while the Reward Responsiveness scale has items that focus on positive responses to the occurrence or anticipation of reward (“liking”), which can be considered more passive. Importantly, these different aspects of approach and reward processing have been related to different neural substrates (Berridge, 2007). Of course, when relating these different aspects of approach behavior to neural activations during rest (with no possibility to act), it may not be so surprising that we find that the more passive aspect of approach and reward processing relates to left RFA. Indeed, it may even be argued that active approach has to be inhibited during rest, which may account for the association between BAS-Fun and BAS-Drive and right RFA.

Nevertheless, it is the left RFA we measured in the resting state that is associated with increased P3 amplitudes on trials requiring a global attentional focus. Enhanced P3 amplitudes for global stimuli are one of the most consistent findings in ERP research on attentional scope and have been proposed to reflect a more efficient process of perceiving, evaluating, and classifying global, as opposed to local, stimuli (Han & Jiang, 2006; Han et al., 1997; Heinze & Münte, 1993; Malinowski et al., 2002; Proverbio et al., 1998; Volberg & Hubner, 2004). Indeed, in the present study we found that this increase in P3 amplitude was related to faster RTs on stimuli requiring a global focus. In addition, we found that subjects with left RFA during rest displayed shorter P3 peak latencies on trials requiring a global focus. As P3 latencies are proposed to reflect the speed of stimulus classification (Duncan-Johnson, 1981), this may provide

additional evidence for the positive association between left RFA during rest and subsequent increased efficiency in processing global information.

In addition, our difference-wave analysis showed that the main ERP effect associated with a global attentional focus was right-lateralized, mirroring earlier findings (e.g., Han et al., 1997; Proverbio et al., 1998). Our results show that this posterior ERP lateralization was especially pronounced for subjects with a left resting-state RFA. Perhaps somewhat surprisingly, this posterior ERP lateralization was unrelated to relative posterior asymmetrical EEG activity as measured during the task (cf. Volberg et al., 2009). We did find however that this right RPA, as measured during task performance, was related to BAS-Drive, and also to fewer errors on trials requiring a global focus, suggesting that subjects high on BAS-Drive may engage right-posterior brain areas to a larger extent, which may result in better performance on global trials.

Finally, we found that global targets elicited a larger N1 compared to local targets (see also Proverbio et al., 1998), except for subjects with a left Rest-RFA, who only did not show this increase in amplitude for global targets when the stimulus was congruent. The N1 attention effect (i.e., larger N1 amplitude for attended stimuli) appears to reflect an enhanced processing of attended stimuli, probably involving a discriminative process that is applied to a restricted area of visual space (Vogel & Luck, 2000). This may explain the finding of larger N1 amplitudes for global stimuli: The area of visual space to which the attentional spotlight has to be applied is larger and there is more visual information to discriminate within this spotlight. Apparently, this is not what happens with subjects with left Rest-RFA; it may be speculated that these subjects do not engage in processing of the visual details (the local features) of the global stimuli when all the information they require is already in the global shape, giving them an advantage in processing congruent local stimuli. When the stimulus is incongruent however, also left Rest-RFA subjects may not be able to inhibit the processing of the local features.

Although there are many studies showing that individual differences in approach motivation and dispositional affect influence attentional scope, such that approach motivation and positive affect lead to a broader focus of attention, while avoidance motivation and negative affect are associated with a more narrow focus of attention (e.g., Förster, Friedman, Ozelsel, & Denzler, 2006; Gasper & Clore, 2002; Kimchi, 1992), some recent studies have reported contradictory results (Gable & Harmon-Jones, 2008), showing that approach-motivated positive affect (induced by viewing pictures of desserts) and left RFA do not lead to broadening but instead to a narrowing of attentional scope.

The present findings may be seen as a starting point to reconcile these different findings. First, we have shown that the association between approach/avoidance motivation and RFA may not be so straightforward as assumed: While BIS displayed the expected pattern of increased right RFA during a rest measurement, only BAS-Reward was shown to be associated with left Rest-RFA, while BAS-Fun and BAS-Drive were even associated with right Rest-RFA. Second, although we found a clear association between left Rest-RFA and

enhanced efficiency in processing global information, we found no direct association between approach motivation and attentional scope: While approach motivation (at least as measured by BAS-Reward) and efficient processing of global information are both related to left Rest-RFA, approach motivation as such was not associated with a global attentional focus.

It could be argued that showing hungry subjects pictures of desserts (as in Harmon-Jones & Gable, 2009; Gable & Harmon-Jones, 2008) would be related to the Drive (“wanting”) aspect of approach (which was actually related to right RFA during rest), while RFA during rest could be more related to the “liking” aspect of approach and reward processing (see Gable & Harmon-Jones (2008) for a similar reasoning). Interestingly, these different aspects of approach may both be reflected by RFA, but different neural generators may underlie these asymmetrical activations (see Tops, Boksem, Luu, & Tucker, 2010). Davidson and colleagues (Davidson & Irwin, 1999) suggest that the left dorsolateral PFC (and other prefrontal areas) are involved in Gray’s BAS and are specifically implicated in approach behavior, while the right dlPFC is proposed to be an important component of the BIS and is related to withdrawal behavior. In turn, this differential activation of left and right PFC is thought to underlie findings of frontal EEG asymmetry (Murphy, Nimmo-Smith, & Lawrence, 2003; Pizzagalli, Sherwood, Henriques, & Davidson, 2005; Shackman et al., 2009). However, also the insular cortex has been proposed to be responsible for asymmetrical cortical activations (Craig, 2005): Especially the left insula has been shown to be activated by various kinds of craving, or “wanting,” including hunger, which may be of particular relevance in the context of stimulating approach in hungry subjects by showing them pictures of desirable foods (Harmon-Jones & Gable, 2008). Also, our results show that the different BAS-subscales are related to attentional focus (via RFA) in very different ways. Not distinguishing between these subscales may have resulted in the observation by Gable and Harmon-Jones (2008) that BAS was related to less efficient processing of global information (i.e., both BAS-Fun and BAS-Drive were related to right RFA, while only BAS-R was related to left RFA, which in turn was related to better global processing). Finally, while Harmon-Jones and Gable (2009) found their effects on RFA induced by affective stimuli, which probably reflects a more state-like measure of motivational orientation and affect (which has also been related to RFA; e.g., Davidson, Ekman, Saron, Senulis, & Friesen, 1990; Harmon-Jones & Sigelman, 2001), most other studies have looked at resting-state RFA and questionnaire measures, which may more reflect a trait measure of motivational orientation and which may lead to different patterns of cortical activation and attentional focus.

In summary, we investigated whether individual differences in approach motivation (as measured by the BIS/BAS-scale) and differences in relative hemispheric activity would be associated with attentional scope. We expected that approach motivation and associated left RFA would be associated with a relatively broad attentional scope, which in turn would be associated with enhanced right-posterior brain activity during task performance. The results showed,

however, that only the BAS-Reward subscale displayed this pattern of activity. The other BAS-subscales even showed the reverse pattern: Just like BIS, BAS-Drive, and BAS-Fun were associated with more right RFA during rest. Nevertheless, it was the left RFA that was associated with increased (right-lateralized) P3 amplitudes and decreased P3 latencies on trials requiring a global focus. Moreover, we found that these increased P3 amplitudes were related to faster RTs on stimuli requiring a global focus. These results provide evidence for a positive association between left RFA during rest, that may be associated with approach motivation and subsequent increased efficiency of brain mechanisms involved in processing global information.

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