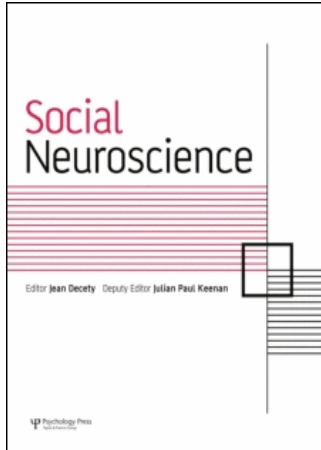


This article was downloaded by:[Peterson, Carly K.]
On: 24 May 2008
Access Details: [subscription number 793187403]
Publisher: Psychology Press
Informa Ltd Registered in England and Wales Registered Number: 1072954
Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Social Neuroscience

Publication details, including instructions for authors and subscription information:
<http://www.informaworld.com/smpp/title~content=t741771143>

Asymmetrical frontal ERPs, emotion, and behavioral approach/inhibition sensitivity

Carly K. Peterson ^a, Philip Gable ^a, Eddie Harmon-Jones ^a
^a Texas A&M University, Texas, USA

First Published on: 11 September 2007

To cite this Article: Peterson, Carly K., Gable, Philip and Harmon-Jones, Eddie (2007) 'Asymmetrical frontal ERPs, emotion, and behavioral approach/inhibition sensitivity', *Social Neuroscience*, 3:2, 113 — 124

To link to this article: DOI: 10.1080/17470910701612736
URL: <http://dx.doi.org/10.1080/17470910701612736>

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Asymmetrical frontal ERPs, emotion, and behavioral approach/inhibition sensitivity

Carly K. Peterson, Philip Gable, and Eddie Harmon-Jones

Texas A&M University, College Station, Texas, USA

The present study sought to extend past research on frontal brain asymmetry and individual differences by examining relationships of individual differences in behavioral inhibition/approach system (BIS/BAS) sensitivity with asymmetrical frontal event-related brain responses to startle probes presented during viewing of affective pictures. One hundred and ten participants were shown unpleasant, neutral, and pleasant affective pictures, and presented startle probes during picture presentations. Individual differences in BIS sensitivity related to relatively greater right frontal N100 amplitude to startle probes presented during pleasant and unpleasant pictures, whereas individual differences in BAS sensitivity related to reduced left frontal P300 amplitude to startle probes presented during pleasant pictures. The results of this study suggest that BIS sensitivity is related to greater relative right frontal cortical activity during affective states, while BAS sensitivity is related to greater relative left frontal cortical activity during appetitive states.

A large portion of the frontal electroencephalographic (EEG) asymmetry literature on individual differences has examined relationships of personality with resting baseline asymmetry. This is due to the widely accepted *dispositional model* of affective style, which states that “individuals are thought to possess a general tendency to predominantly respond with either approach (indexed by relatively greater left frontal activity) or withdrawal (indexed by relatively greater right frontal activity) related affect across all or most situations” (Coan, Allen, & McKnight, 2006, p. 1). In support of this model, greater left than right frontal cortical activity at resting baseline relates inversely with depression (Henriques & Davidson, 1990; Jacobs & Snyder, 1996), directly with positive activation, and

inversely with negative activation (Jacobs & Snyder, 1996; Tomarken, Davidson, Wheeler, & Doss, 1992).

Behavioral approach and inhibition systems

Because the theoretical model guiding many investigations of asymmetrical frontal activity was built on approach/withdrawal motivation, researchers examined the relationship between resting asymmetrical frontal cortical activity and constructs more directly related to approach and withdrawal motivation. One dimension, the *behavioral approach system* (Gray, 1981, 1987, 1990) or the *behavioral activation system* (BAS; Fowles,

Correspondence should be addressed to: Carly Peterson, Texas A&M University, Department of Psychology, 4235 TAMU, College Station, TX 77843, USA. E-mail: carlypeterson@gmail.com

This research was supported by a grant from the National Science Foundation (BCS 0350435).

We gratefully acknowledge the technical support provided by Ziggy Bialzik. We also thank Meghan Fearn and Lacey Lueck for their help with this research, and Cindy Harmon-Jones and Brandon Schmeichel for their helpful suggestions during the preparation of this manuscript. The experiment was run using DmDX software developed at Monash University and at the University of Arizona by Kenneth J. Forster and Jonathan C. Forster.

1980), has been hypothesized to be sensitive to signals of reward, nonpunishment, and avoidance of punishment. Activation of this system creates goal-seeking behavior in individuals, causing them to begin (or increase) movement towards goals. Another dimension related to aversive motivation has been called the *behavioral inhibition system* (BIS; Gray, 1981, 1987, 1990). BIS inhibits behavior, increases arousal, prepares for vigorous behavior, and increases attention to aversive stimuli.

Individuals differ in the sensitivity of the BIS and BAS, and instruments have been developed to tap these individual differences. Carver and White (1994) developed one such instrument and it has been used widely. Research has found that individuals who score high in BAS sensitivity also score higher in anger, physical aggression (Harmon-Jones, 2003), extraversion, hypomania (Harmon-Jones et al., 2002), novelty seeking, and optimism (Carver & White, 1994). They also score lower in harm avoidance (Carver & White, 1994). Individuals who score high in BIS sensitivity score higher in susceptibility to punishment, harm avoidance, and anxiety (Carver & White, 1994). They also score lower on optimism (Carver & White, 1994) and physical aggression (Harmon-Jones, 2003). Further research has suggested that BIS/BAS sensitivity is related to emotional experience. Individuals high in BAS sensitivity report more happiness during and after a rewarding task, while individuals high in BIS sensitivity report more nervousness before and during an uncomfortable task (Carver & White, 1994). Also, individuals high in BAS sensitivity, as compared to those low in BAS sensitivity, show more startle eyeblink inhibition during pleasant pictures, consistent with the conception that inhibition of startle eyeblinks reflects greater appetitive motivation (Hawk & Kowmas, 2003). Additionally, BIS sensitivity has been shown to predict self-rated levels of anxiety in response to fear-related stimuli (Leen-Feldner, Zvolensky, & Feldner, 2004). Finally, highly BIS-sensitive individuals are more likely to identify with a submissive rather than dominant character (Demaree, Robinson, Everhart, & Youngstrom, 2005).

Research has examined the relationship of the BIS/BAS dimensions with asymmetrical frontal cortical activity at resting baseline. Results have indicated that increased relative left frontal cortical activity at baseline relates directly with BAS sensitivity (Coan & Allen, 2003; Harmon-

Jones & Allen, 1997; Sutton & Davidson, 1997). However, relationships of BIS with asymmetrical frontal cortical activity have been inconsistent. One study found BIS sensitivity related to increased relative right frontal cortical activity at resting baseline (Sutton & Davidson, 1997), whereas two others found no relationship between frontal asymmetry and BIS sensitivity (Coan & Allen, 2003; Harmon-Jones & Allen, 1997).

There have been failures to replicate some of the findings of relationships between resting baseline asymmetry and affective traits and responses (see Coan & Allen, 2004, for a review), possibly because asymmetrical frontal cortical activity is also sensitive to state manipulations (e.g., Hagemann, Naumann, Becker, Maier, & Bartussek, 1998; Reid, Duke, & Allen, 1998). In fact, much of the variance in baseline resting measurements is state rather than trait variance (Hagemann, Naumann, Thayer, & Bartussek, 2002).

To address these concerns, Coan, Allen, and McKnight (2006) proposed a *capability model* of frontal EEG asymmetry and personality, which hypothesizes that there are meaningful individual differences in frontal EEG asymmetry, but that individuals have different capabilities in terms of approach versus withdrawal responses depending on the demands of the specific situation. Simply using resting baseline EEG to predict personality is not enough, given that personality is best evident when elicited in particular states or situations (Wallace, 1966). This may explain why BIS sensitivity has not been found to consistently relate to relative right frontal cortical activity (Coan & Allen, 2003; Harmon-Jones & Allen, 1997). BIS sensitivity may relate more strongly to relative right frontal activation during the activation of a negative, withdrawal-related emotion than in a neutral or resting state.

Measurements of asymmetrical frontal cortical activity

Most previous studies examining emotion and frontal asymmetry have used alpha power derived from the electroencephalogram (EEG) as a measure of brain activity, because activity within the alpha range (8–13 Hz) is inversely related to underlying cortical activity (see Lindsley & Wicke, 1974, for a review). Some research using

PET and fMRI has also found asymmetrical activations in frontal brain regions during emotional and motivational states (see Pizzagalli, Shackman, & Davidson, 2003, for a review). To our knowledge, there are only a few studies examining emotional processes and frontal asymmetry using event-related potentials (ERPs). In one such study, Cunningham, Espinet, DeYoung, and Zelazo (2005) measured the late positive potential (LPP) while participants made evaluative (good vs. bad) and non-evaluative (abstract vs. concrete) judgments about socially relevant concepts. The concepts were then rated for goodness and badness. Concepts rated bad caused greater LPPs over the right frontal hemisphere, while concepts rated good caused greater LPPs over the left frontal hemisphere. Graham and Cabeza (2001) found larger left frontal ERPs (as measured by a window of 750 ms to 1250 ms after event onset) during the viewing of unfamiliar happy faces and larger right frontal ERPs during unfamiliar neutral faces.

Past research revealed that amplitudes of two ERPs recorded along the midline are involved in affective processing (Cuthbert, Schupp, Bradley, McManis, & Lang, 1998; Schupp, Cuthbert, Bradley, Birbaumer, & Lang, 1997). The N100 component of the ERP, which is a negative wave present approximately 100 ms after event onset, is related to automatic selective attentional processing. Auditory N100 amplitude is potentiated by increased attention to the stimuli (Hillyard, Hink, Schewent, & Picton, 1973). The P300 component, which is a positive wave that occurs around 300 ms after event onset, is related to updating of working memory (Donchin & Coles, 1988). In the past research, the elicited startle eyeblink reflex and event-related potentials were recorded while participants viewed emotionally evocative pictures (Cuthbert et al., 1998). Eyeblink magnitude varied as a function of picture pleasantness, with potentiated startle reflexes occurring when the probe was presented during unpleasant pictures and inhibited reflexes occurring when the probe was presented during pleasant pictures. P300 amplitude to the startle probe was reduced while viewing pleasant and unpleasant pictures as compared to neutral pictures, regardless of whether participants were instructed to attend to, or ignore, the startle probes. N100 amplitude to the startle probe during unpleasant as compared to other picture types was significantly increased when participants were instructed to attend to the startle probes, but no affective

modulation was detected when participants were instructed to ignore startle probes.

Cuthbert et al. (1998) hypothesized that more “working memory” resources are needed when processing emotional pictures, and that the P300 is diminished because fewer resources are available to process the probe stimulus. Because the N100 component relates to selective attentional processing, the increased N100 response during unpleasant pictures supports the idea that early cortical processing is activated by aversive motivation. However, these N100 effects occurred only when participants were instructed to attend to the startle probe.

Present research

The present study examined the effect of BIS/BAS sensitivity on frontal asymmetry during the viewing of emotional pictures. Over 70 published studies have examined the relationship between frontal brain asymmetry and emotion or emotion-related constructs (see Coan & Allen, 2004, for a review), and we sought to extend this past work by examining frontal asymmetries in the N100 and P300 ERP components to startle probes. We hypothesized that individuals high in BIS sensitivity, who are high in anxiety (Carver & White, 1994), would show increased N100 amplitude over the right frontal cortical region while viewing unpleasant stimuli, even when not given specific instructions to attend to the probe. This prediction was predicated on past research and theory that suggests that anxious individuals may selectively process threat-related stimuli. We also hypothesized that individuals high in BIS sensitivity would show reduced right-frontal P300 amplitudes while viewing unpleasant stimuli, indicating that more “working memory” resources were being spent processing the picture rather than the probe.

For individuals high in BAS sensitivity, who are more sensitive to rewards and approach-evoking stimuli, we predicted that they would show reduced P300 while viewing pleasant stimuli, indicating that more “working memory” resources were being spent processing the picture rather than the probe. These effects were predicted to be evident over the left frontal cortex, a region that is hypothesized to be involved in approach motivational processes. Because the N100 response to the startle probe has only been found to be enhanced during selective

attention to unpleasant stimuli (Cuthbert et al., 1998), individual differences in BAS sensitivity were not expected to relate to N100 amplitudes.

In addition to extending past research, we also expected to replicate previous findings on ERP and startle eyeblink amplitude to startle probes during affective pictures (Cuthbert et al., 1998; Schupp et al., 1997).

METHOD

Participants

One hundred ten (40 men, 70 women) right-handed introductory psychology students at a university in the middle of the United States participated in exchange for extra credit.¹

Materials

Forty-eight pictures were presented in randomized order; 16 selected from each of the unpleasant (e.g., snake, bloody hand), neutral (e.g., spoon, rolling pin), and pleasant (e.g., windsailing, partially nude couple) types of the International Affective Picture System (Center for the Study of Emotion and Attention, 1995).² Three neutral picture practice trials preceded the 48 pictures. Each picture trial consisted of a fixation cross presented for 1 second, a picture presented for 6 seconds, and an ITI of 14–19 seconds.

The startle probe was a 50 ms, 102 dB burst of white noise presented through stereo headphones. Probes were presented 3.5 or 4.5 seconds after picture onset. The 3.5 and 4.5 second probes were varied in order to prevent the individual from learning when the probe would occur and combined for analyses, as is commonly done in startle probe affective picture research (e.g., Patrick, Bradley, & Lang, 1993).

¹ An additional 28 participants were run but their data were not analyzed, because of equipment problems: 16 were due to failed startle eyeblink collection, 9 were due to failed EEG collection, and 3 were due to no self-report measures.

² IAPS picture numbers: 1050, 1090, 1200, 1300, 2190, 2200, 2240, 2440, 2480, 2500, 2620, 2850, 2880, 3060, 3150, 3400, 3550, 4672, 4608, 4611, 4641, 4653, 4658, 4659, 4670, 5470, 5500, 5621, 5626, 5731, 6230, 7000, 7004, 7006, 7010, 7020, 7031, 7080, 7175, 7270, 7380, 8080, 8170, 8190, 8370, 9250, 9300, 9405, 9500, 9620, and 9630.

Carver and White's (1994) 20-question BIS/BAS scale was administered to assess individual differences in BIS and BAS sensitivity. It is comprised of four scales: BIS, which has seven items that measure reactions to the expectation of punishment; BAS drive, which contains four items that pertain "to the persistent pursuit of desired goals"; BAS reward responsiveness, which contains five items that "focus on positive responses to the occurrence or anticipation of reward"; and BAS fun seeking, which has four items "reflecting both a desire for new rewards and a willingness to approach a potentially rewarding event on the spur of the moment" (p. 322).

For the present sample, the Cronbach alphas for reliability for each subscale were: BIS = .80, BAS-Total = .72, BAS-Drive = .75, BAS-Fun = .74, BAS-Reward Responsiveness = .51.

Procedure

After informed consent was obtained, participants completed the BIS/BAS questionnaire. Electrodes were affixed to their face and scalp. Participants then viewed pictures in randomized order while EEG and EMG over the left inferior orbicularis oculi (startle eyeblinks) were recorded. Participants were told to ignore the intermittent noises they would hear through the headphones, as was done in most past startle eyeblink research.

Data collection and reduction

To record EEG, 27 tin electrodes mounted in a stretch-lycra electrode cap (Electro-Cap, Eaton, OH) were placed on the participant's head. The reference electrode was placed on the left earlobe, and data were acquired from an electrode on the right earlobe, so that an off-line, averaged ears' reference could be computed. Vertical and horizontal eye movements (EOG) were also recorded to facilitate artifact correction of the EEG. All electrode impedances were under 5 k Ω , and homologous sites were within 1 k Ω of each other.

EEG and EOG were amplified with Neuroscan Synamps (El Paso, TX), bandpass filtered (0.1 to 100 Hz; 60 Hz notch filter enabled) and digitized at 500 Hz. The signals were visually scored and portions of the data that contained artifacts were removed. A regression-based eye movement

correction was then applied (Semlitsch, Anderer, Schuster, & Presslich, 1986), after which the data were visually inspected, to insure that proper correction was done. Then, the data were band-pass filtered at 35 Hz to facilitate peak detection. Group averages were computed for each picture type, and the ERP waveforms were visually scored to determine the windows used during peak detection. The N100 base-to-peak of the ERP was derived as the maximum negative deflection within a window of 50–150 ms following the onset of each startle probe; the P300 was scored as base-to-peak amplitude within a window of 250–350 ms following the onset of each startle probe.

To record startle eyeblinks, 4 mm Ag/AgCl electrodes (In Vivo Metric, Healdsburg, CA) were placed over the left inferior orbicularis oculi below the inner and outer canthi, as suggested by Van Boxtel, Boelhouwer, and Bos (1998). Impedance levels were 10 k Ω or below. The electromyographic (EMG) signal was amplified, and frequencies below 30 Hz and above 500 Hz were filtered online (Contact Precision Instruments Bio II, Cambridge, MA). Signals were digitally sampled at 1000 Hz. Offline, EMG activity was rectified and then smoothed. The peak magnitude following the onset up to 120 ms was determined.

RESULTS

New findings

Asymmetrical frontal ERP

Relationships with BIS/BAS sensitivity. Because past research has suggested that BIS/BAS sensitivity should relate to right/left mid-frontal (F3/4) brain activity (e.g., Harmon-Jones & Allen, 1997; Sutton & Davidson, 1997), we examined whether asymmetrical ERPs over mid-frontal sites during affective picture viewing varied with BIS/BAS sensitivity. All other asymmetry indexes were also examined, to assess whether the predicted effects were specific to the mid-frontal sites. For both ERPs, higher scores on the asymmetry indexes indicate greater left than right hemispheric amplitudes. Because N100 has a negative amplitude, asymmetry indexes were created by subtracting amplitude at left site from amplitude at right site (F4–F3). Asymmetry indexes for P300, which has a positive amplitude, were created by subtracting

amplitude at right site from amplitude at left site (F3–F4).

Zero-order correlations. Individuals with greater BIS sensitivity evidenced lower scores on the mid-frontal N100 asymmetry index to startle probes during both unpleasant, $r(108) = -.28, p < .01$, and pleasant, $r(108) = -.21, p < .05$, pictures, indicating greater right than left hemispheric N100 amplitudes.³ A similar relationship was found between BIS sensitivity and lateral frontal N100 asymmetry to startle probes during unpleasant, $r(108) = -.20, p < .05$, pictures (the BIS/N100 to startle probes during pleasant pictures relationship was negative but marginal, $p > .06$). There were no other significant relationships between BIS or BAS sensitivity and N100 asymmetry to startle probes during affective pictures, $ps > .09$.

For the mid-frontal P300 asymmetry index, individuals with greater BAS sensitivity evidenced lower scores to startle probes during pleasant pictures, $r(108) = -.22, p < .05$, indicating greater relative right than left frontal P300 amplitude. Based on previous interpretations of the P300 wave (e.g., Cuthbert et al., 1998), these results suggest that individuals high in BAS sensitivity have less cortical activity over the left mid-frontal region in response to the probe because they are using more of these cortical resources to process the picture. Similarly, individuals high in BAS reward responsiveness evidenced lower scores on the anterior-temporal P300 asymmetry index to startle probes during pleasant pictures, $r(108) = -.18, p < .05$. Both BAS and BAS drive sensitivity related to anterior-temporal (T3/4) P300 asymmetry to startle probes during unpleasant pictures, $r(108) = .19, p < .05$ and $r(108) = .22, p < .05$, respectively. There were no other significant relationships between BIS or BAS sensitivity and P300 asymmetry to startle probes during affective pictures, $ps > .07$.

Regressions controlling for neutral picture ERPs. To examine whether affective pictures

³ To assess whether gender affected the ERP responses, we conducted regression analyses in which centered BIS/BAS scores, gender, their interaction, and the response to startle probes during neutral pictures were entered as predictors of a given ERP response. The interaction of gender and BIS sensitivity did not predict any ERP responses when controlling for ERP responses to startle probes during neutral pictures.

per se exerted effects on the frontal asymmetrical N100 responses, regressions were conducted in which the asymmetrical N100 response to the neutral picture (at a given region) served as a statistical control in the relationship of BIS/BAS and affective picture type. If a significant asymmetrical N100—individual difference (BIS/BAS sensitivity) partial correlation was observed, follow-up tests were conducted on each hemisphere, to examine whether the right or left hemisphere or both were related to BIS/BAS sensitivity.

Controlling for neutral picture responses, BIS sensitivity related inversely to N100 mid-frontal asymmetry to startle probes during unpleasant pictures, $\beta = -.22$, partial $r(108) = -.29$, $t(107) = -3.1$, $p < .05$, and pleasant pictures, $\beta = -.14$, partial $r(108) = -.22$, $t(107) = -2.1$, $p < .05$. That is, individuals with greater BIS sensitivity had greater relative right mid-frontal N100 amplitude to startle probes during unpleasant and pleasant pictures. Follow-up tests revealed a significant relationship between BIS sensitivity and N100 amplitude over the right mid-frontal region to startle probes during unpleasant pictures, $\beta = -.14$, partial $r(108) = -.20$, $t(107) = -2.2$, $p < .05$, but not during pleasant pictures, $\beta = -.08$, partial $r(108) = -.10$, $t(107) = -1.1$, $p = .28$. For the left mid-frontal region, no significant relationships were found between BIS sensitivity and N100 amplitude to startle probes during either picture type, unpleasant: $\beta = -.03$, partial $r(108) = -.05$, $t(107) = -0.5$, $p > .61$; pleasant: $\beta = -.03$, partial $r(108) = -.04$, $t(107) = -0.45$, $p = .66$.

To examine whether BIS was more strongly related to mid-frontal asymmetrical N100 amplitude to startle probes during unpleasant than during pleasant pictures, regression analyses were conducted in which BIS and mid-frontal asymmetrical N100 to startle probes during one affective picture type (pleasant pictures) predicted mid-frontal asymmetrical N100 to startle probes during the other affective picture type (unpleasant pictures). When BIS and N100 asymmetry to startle probes during pleasant pictures were used to predict N100 asymmetry to startle probes during unpleasant pictures, both predictors were significant, BIS: $\beta = -.15$, partial $r(108) = -.19$, $t(107) = -2.1$, $p < .05$; N100 to pleasant pictures: $\beta = .65$, partial $r(108) = .66$, $t(107) = 9.1$, $p < .001$. In contrast, when BIS and N100 asymmetry to startle probes during unpleasant pictures were used to predict N100 asymmetry to startle probes during pleasant pictures, only N100 asymmetry to

startle probes during unpleasant pictures was a significant predictor, $\beta = .67$, partial $r(108) = .66$, $t(107) = 9.1$, $p < .001$; BIS: $\beta = -.02$, partial $r(108) = -.03$, $t(107) = -0.28$, $p = .78$. These results suggest that BIS was more strongly related with N100 mid-frontal asymmetry to startle probes during unpleasant than pleasant pictures.

As expected, BAS sensitivity did not relate to asymmetrical frontal N100 amplitude to startle probes during unpleasant or pleasant pictures ($ps > .38$). To further establish that BIS per se related to asymmetrical frontal N100 responses, a regression analysis with BIS, BAS, and N100 to neutral pictures as predictors of N100 to startle probes during unpleasant pictures revealed that only BIS, $\beta = -.22$, partial $r(108) = -.29$, $t(107) = -3.1$, $p < .01$, and N100 to startle probes during neutral pictures, $\beta = .64$, partial $r(108) = .66$, $t(107) = 9.1$, $p < .001$, were significant predictors, and BAS was not, $\beta = -.02$, partial $r(108) = -.02$, $t(107) = -0.23$, $p = .82$. A similar regression analysis with BIS, BAS, and N100 to startle probes during neutral pictures as predictors of N100 to startle probes during pleasant pictures revealed that only BIS, $\beta = -.14$, partial $r(108) = -.19$, $t(107) = -2.0$, $p < .05$, and N100 to startle probes during neutral pictures, $\beta = .67$, partial $r(108) = .68$, $t(107) = 9.4$, $p < .001$, were significant predictors, and BAS was not, $\beta = .01$, partial $r(108) = .01$, $t(107) = 0.11$, $p = .92$.

Because asymmetrical lateral frontal N100 amplitude responses to startle probes during unpleasant and neutral pictures related to BIS in zero-order correlations, we examined whether asymmetrical lateral frontal N100 amplitude to startle probes during unpleasant pictures related to BIS when controlling for asymmetrical lateral frontal N100 amplitude to startle probes during neutral pictures. Results from a regression analysis testing this pattern of relationships revealed that BIS was not related to asymmetrical lateral frontal N100 amplitude to startle probes during unpleasant pictures when controlling for asymmetrical lateral frontal N100 amplitude to startle probes during neutral pictures ($p > .25$).

As done previously with the BIS/N100 relationships, regressions were conducted in which the asymmetrical P300 response to startle probes during the neutral picture (at a given region) served as a statistical control in the relationship of BIS/BAS and affective picture type. If a significant asymmetrical P300—individual difference (BIS/BAS sensitivity) partial correlation was observed, follow-up tests were conducted on each

hemisphere, to examine whether the right or left hemisphere or both were related to BIS/BAS sensitivity.

BAS sensitivity related significantly to mid-frontal P300 asymmetry to startle probes during pleasant pictures, $\beta = -.19$, partial $r(108) = -.19$, $t(107) = -2.0$, $p < .05$. Individuals with greater BAS sensitivity had less relative left mid-frontal P300 amplitude to startle probes during pleasant pictures. Follow-up tests revealed a significant inverse relationship between BAS sensitivity and P300 amplitude to startle probes during pleasant pictures over the left mid-frontal region, $\beta = -.16$, partial $r(108) = -.20$, $t(107) = -2.1$, $p < .05$, indicating reduced left mid-frontal P300 amplitude. Right mid-frontal P300 amplitude did not relate to BAS sensitivity ($p = .21$). These results are consistent with the idea that these individuals use working memory resources in the left mid-frontal region to process the picture rather than to process the startle probe.

BIS sensitivity did not relate to asymmetrical frontal P300 amplitude to startle probes during unpleasant or pleasant pictures ($ps > .17$). To further establish that BAS per se related to asymmetrical frontal P300 responses, a regression analysis with BAS, BIS, and P300 to startle probes during neutral pictures as predictors of P300 to startle probes during pleasant pictures revealed that only BAS, $\beta = -.20$, partial $r(108) = -.21$, $t(107) = -2.2$, $p < .05$, and P300 to startle probes during neutral pictures, $\beta = .25$, partial $r(108) = .25$, $t(107) = 2.7$, $p < .01$, were significant predictors, and BIS was not, $\beta = -.14$, partial $r(108) = -.15$, $t(107) = -1.6$, $p > .12$.

Because zero-order correlations also revealed significant relationships between BAS variables and anterior-temporal P300 asymmetry, we also conducted exploratory analyses at that region. However, because the focus of our research was to examine asymmetrical frontal ERPs, the analyses were not as in-depth as done previously. BAS reward responsiveness related significantly to anterior-temporal P300 asymmetry to startle probes during pleasant pictures, $\beta = -.23$, partial $r(108) = -.26$, $t(107) = -2.8$, $p < .01$. Follow-up tests revealed a significant inverse relationship between BAS reward responsiveness and P300 amplitude to startle probes during pleasant pictures over the left anterior-temporal region, $\beta = -.20$, partial $r(108) = -.27$, $t(107) = -2.9$, $p < .01$. Right anterior-temporal P300 amplitude did not relate to BAS reward responsiveness ($p = .93$). BAS drive related significantly to anterior-

temporal P300 asymmetry to startle probes during unpleasant pictures, $\beta = .19$, partial $r(108) = .21$, $t(107) = 2.3$, $p < .05$. However, follow-up tests did not reveal any significant relationships between BAS drive and P300 amplitude at either hemisphere ($ps > .21$). While BAS sensitivity also related significantly to anterior-temporal P300 asymmetry to startle probes during unpleasant pictures in simple, zero-order correlations, when statistically controlling for neutral P300 asymmetry the relationship was only marginal, $\beta = .15$, partial $r(108) = .17$, $t(107) = 1.8$, $p > .07$.

Analyses without consideration of individual differences. We examined whether left and right frontal site ERPs (F3 and F4) differed as a function of picture type. The 3 (Affect: unpleasant, neutral, pleasant) \times 2 (Hemisphere: left, right) ANOVA for N100 amplitude did not reveal any significant overall effects involving affective pictures ($ps > .32$). The ANOVA for P300 amplitude revealed only a main effect of picture type, $F(2, 218) = 17.8$, $MSE = 42.8$, $p < .001$ (other $ps > .81$). All three picture types differed significantly from each other ($ps < .05$), with greater P300 amplitudes to startle probes during neutral pictures ($M = 19.8$, $SE = 0.7$), followed by unpleasant pictures ($M = 17.4$, $SE = 0.7$), and lastly pleasant pictures ($M = 16.1$, $SE = 0.7$). See Figures 1 and 2 for average waveforms at F3 and F4.

Replicated findings

Startle eyeblink magnitude

An ANOVA revealed that startle eyeblink was significantly modulated by picture valence,

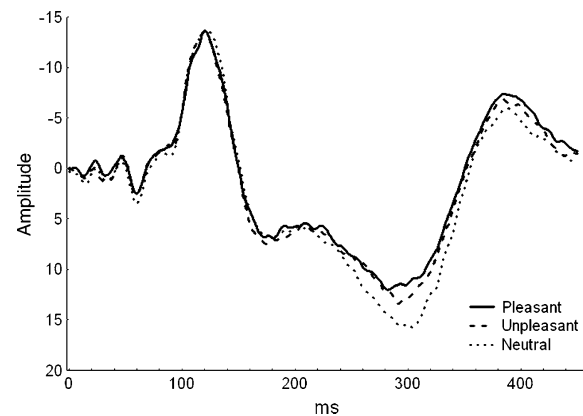


Figure 1. Average waveforms for all participants at right mid-frontal (F4) site during picture viewing.

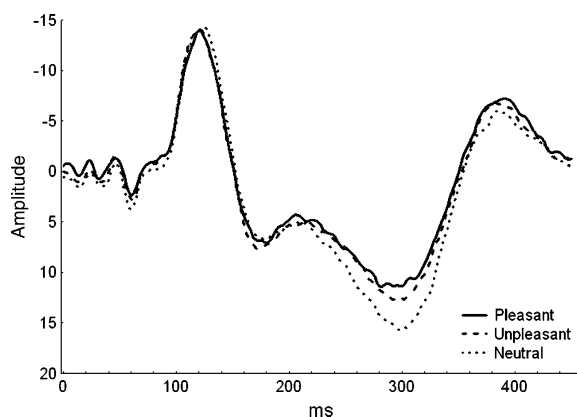


Figure 2. Average waveforms for all participants at left mid-frontal (F3) site during picture viewing.

$F(2, 218) = 45.0$, $MSE = 64.3$, $p < .001$. Eyeblinks were greatest for unpleasant pictures ($M = 35.3$, $SE = 3.3$) and smallest for pleasant pictures ($M = 25.1$, $SE = 2.8$), with neutral picture blinks in between the other two ($M = 29.3$, $SE = 2.9$; $ps < .001$). These effects replicate past research (e.g., Bradley, Cuthbert, & Lang, 1993; Cuthbert et al., 1998; Lang, Bradley, & Cuthbert, 1990; Schupp et al., 1997).

Midline ERPs

P300. Consistent with earlier findings (Cuthbert et al., 1998; Schupp et al., 1997), a 3 (Affect: unpleasant, neutral, pleasant) \times 3 (Midline Location: Fz, Cz, Pz) ANOVA found that the P300 wave was significantly modulated by picture valence, $F(2, 218) = 24.8$, $MSE = 75.4$, $p < .001$. P300 amplitude was greatest when viewing neutral pictures as compared to unpleasant pictures and pleasant pictures ($ps < .001$).

A main effect for location was also found, $F(2, 218) = 215.0$, $MSE = 57.6$, $p < .001$. P300 amplitude was greatest at Cz and smallest at Fz, with Pz in between ($ps < .001$), which is also consistent with previous research (Cuthbert et al., 1998; Schupp et al., 1997).

The modulation of the P300 by picture pleasantness varied marginally across electrode sites, $F(4, 436) = 2.3$, $MSE = 8.4$, $p < .06$. To further examine this, additional ANOVAs were conducted for each location. At Fz, P300 amplitude varied by picture valence, $F(2, 218) = 17.6$, $MSE = 25.0$, $p < .001$. Amplitude was greatest during neutral pictures ($p < .001$), and unpleasant and pleasant pictures did not differ significantly ($p > .09$). At Cz, P300 amplitude also varied by

picture valence, $F(2, 218) = 20.0$, $MSE = 34.9$, $p < .001$. Amplitude was greatest during neutral pictures and smallest during pleasant pictures, with unpleasant pictures in between ($ps < .001$). Finally, at Pz, P300 amplitude also varied by picture valence, $F(2, 218) = 23.9$, $MSE = 32.4$, $p < .001$. Like Fz, amplitude was greatest during neutral pictures ($p < .001$), but no differences were found between unpleasant and pleasant pictures ($p > .30$).

N100. A 3 (Affect: unpleasant, neutral, pleasant) \times 3 (Midline Location: Fz, Cz, Pz) ANOVA revealed that the N100 wave was significantly affected by picture valence, $F(2, 218) = 3.2$, $MSE = 48.0$, $p < .05$. N100 amplitude was greater during neutral pictures as compared to unpleasant pictures ($p < .05$). A main effect for location was also evident, $F(2, 218) = 161.9$, $MSE = 77.3$, $p < .001$. N100 amplitude was greatest at Cz and smallest at Pz, with Fz in between ($ps < .001$).

N100 amplitude varied by picture valence as a function of location, $F(4, 436) = 2.6$, $MSE = 8.5$, $p < .05$. To examine this further, ANOVAs were conducted at each location. At Cz, N100 amplitude varied significantly by picture valence, $F(2, 218) = 5.3$, $MSE = 23.5$, $p < .01$. Amplitude was smallest during pleasant pictures compared to neutral ($p < .01$) and unpleasant pictures ($p < .07$). No differences were found between neutral and unpleasant pictures ($p > .17$). Picture valence did not affect N100 amplitude at Fz or Pz ($ps > .12$). Absolute values of amplitude means for midline ERPs can be found in Table 1.

TABLE 1

Absolute values of P300 and N100 mean amplitudes (standard errors) for unattended startle probes during picture presentation

ERP	Picture type	Location		
		Fz	Cz	Pz
P300	Unpleasant	19.5 (0.9) _a	31.6 (1.2) _a	26.8 (1.0) _a
	Neutral	22.3 (0.9) _b	34.9 (1.1) _b	30.9 (1.0) _b
	Pleasant	18.4 (0.8) _a	29.9 (1.1) _c	26.0 (0.9) _a
N100	Unpleasant	20.1 (0.9) _a	25.7 (1.1) _a	12.9 (0.7) _a
	Neutral	20.5 (0.9) _a	26.6 (1.1) _a	13.9 (0.7) _a
	Pleasant	19.2 (0.8) _a	24.5 (1.0) _b	13.2 (0.8) _a

Note: For each electrode location and ERP component, means that are significantly different from each other are denoted by different subscripts.

DISCUSSION

Summary of new findings

The present study extended past work by showing that startle-related N100 amplitude is modulated by affective picture type for individuals high in BIS sensitivity. Whereas previous results suggested that N100 was modulated by negative affective pictures *only* when participants were instructed to attend to the startle probe, the current results suggest that individuals with high BIS sensitivity show greater right frontal N100 amplitudes to affective pictures even when they are explicitly instructed to not attend to the startle probe. Perhaps their excessive sensitivity to arousal (Watson, Weber, Assenheimer, & Clark, 1995) makes high BIS individuals more attuned to stimuli that evoke defensive responses (startles) during arousing states (unpleasant or pleasant pictures).

The present research also extended past work by showing that BAS sensitivity modulates startle-related P300 amplitude. It suggests that individuals high in BAS sensitivity show reduced left frontal P300 responses to startle probes during pleasant pictures, indicating more working memory resources are being dedicated to processing the picture. This is most likely because individuals high in BAS sensitivity respond to appetitive stimuli, such as pleasant pictures, with approach motivation. The fact that this relationship was only over the left frontal region provides even more support for this idea, because past research has already demonstrated links between the left prefrontal cortex and approach motivation (Coan & Allen, 2003; Harmon-Jones & Allen, 1997; Sutton & Davidson, 1997).

Summary of replicated findings

The present study replicated past research by showing that picture valence affects startle eye-blink magnitude, with the reflexive blink being largest for unpleasant pictures and smallest for pleasant pictures (e.g., Bradley et al., 1993; Cuthbert et al., 1998; Lang et al., 1990; Schupp et al., 1997). It also replicated past research showing that midline P300 amplitude is reduced while viewing pleasant and unpleasant pictures as compared to neutral pictures (e.g., Cuthbert et al., 1998; Schupp et al., 1997). In the present study,

N100 amplitude at Cz was smaller to pleasant pictures than to other pictures. Past research revealed no N100 amplitude differences as a function of picture type (Cuthbert et al., 1998). However, inspection of Figure 1 of Cuthbert et al. (1998) suggests a pattern of results similar to the present study. In Cuthbert et al. (1998) this effect was not significant with 40 participants, but was significant in the present study with 110 participants. Perhaps the difference in sample size provided the statistical power to detect this N100 amplitude difference at Cz.

BIS and N100 responses to negative and positive pictures: Emotionality hypothesis

The results regarding BIS and N100 responses to startle probes during unpleasant pictures were in accord with predictions. However, the results with BIS and N100 responses to pleasant pictures were unexpected. The results with the pleasant stimuli suggest the possibility that individuals high in BIS sensitivity may respond to appetitive stimuli (e.g., arousing pleasant pictures) with withdrawal-oriented attentional responses. This is consistent with the *emotionality hypothesis* (Martin, Williams, & Clark, 1991), which states that individuals high in trait anxiety (who are likely high in BIS sensitivity; Carver & White, 1994) are more likely to selectively process any emotional information, not just that which is negative in valence. Previous research supports this hypothesis, showing that highly anxious individuals evidence longer Stroop response latencies to both negative and positive stimuli in relation to neutral stimuli (e.g., Chen, Lewin, & Craske, 1996; McNally, Mogg, & Millar, 2000).

However, research on the emotionality hypothesis is not consistent across studies. Some studies have been supportive and some have not (see Ruiz-Caballero & Bermudez, 1997, for a review). In the present study, the relationship between BIS and right frontal N100 amplitude was stronger during unpleasant pictures than during pleasant pictures. This is consistent with the prediction that BIS sensitivity would predispose individuals to attend selectively toward negative stimuli and such selective attention would be implemented in the right frontal cortical region. Moreover, the current results suggest that past inconsistencies may be due to sample size, power issues, and measurement sensitivity. That

is, in the present study, an anxiety-related dimension—BIS—related to attentional responses to both unpleasant and pleasant stimuli, but the relationship was stronger for unpleasant than pleasant stimuli. Depending on the sample size and sensitivity of the attention measure, the latter relationship may be significant or non-significant.

Implications of BIS–N100 and BAS–P300 results

The present results add to our understanding of the relation between BIS sensitivity and relative right frontal brain activity. They suggest that such a relation may be more likely to emerge during the elicitation of affective states as compared to measurement of resting baseline activity. These results provide support for the capability model of EEG asymmetry (Coan et al., 2006), and suggest that enhanced understanding of the relationship between personality characteristics and asymmetrical frontal cortical activity may result from measuring the effects of personality characteristics on cortical responses during situations or states relevant to the personality characteristic of interest.

BAS sensitivity and asymmetrical N100 relationships were not significant; however, BAS sensitivity did relate to P300 responses. Whereas BAS sensitivity has been found to relate to resting baseline frontal asymmetry in past work, the present study revealed that BAS sensitivity was not related to asymmetrical N100 responses during affective pictures. On the other hand, BIS sensitivity has mostly *not* been found to relate to resting baseline frontal asymmetry in past work, but in the present study, it related to asymmetrical N100 responses during affective pictures.

N100 amplitude likely taps a different psychological construct than regional EEG alpha power. N100 has been found to be associated with selective attention, whereas alpha power over the frontal cortices has been found to be associated with motivational intensity or action readiness (Harmon-Jones, Lueck, Fearn, & Harmon-Jones, 2006). Perhaps this explains why BIS relates to N100 over the right frontal cortex, whereas BAS relates to alpha power over the left frontal cortex. Such an interpretation would be consistent with the idea that BAS is more involved in the activation of behavior and goal-directed movement,

whereas BIS is more involved in the inhibition of behavior and the increase of attention to aversive stimuli (Fowles, 1980; Gray, 1981, 1987, 1990). Alpha power over the left frontal cortex may be tapping this behavioral approach response, whereas N100 over the right frontal cortex may be tapping this inhibitory attentional response.

The fact that BAS sensitivity related to P300 amplitude suggests that the P300 may hold similar qualities as EEG alpha power. Past work has suggested that P300 amplitude assesses working memory. The current results linking BAS to left frontal P300 responses during appetitive pictures is consistent with recent work suggesting connections between motivational responses and working memory processes implicated in asymmetrical frontal cortical regions (Gray, 2001). Also, some might question whether the asymmetrical P300 response observed at frontal sites is indeed a P300 response. Past research has suggested that the maximal parietal P300 and maximal frontal P300 (sometimes called the “P3b” and “P3a,” respectively) have two distinct generators, leading to anatomical, pharmacological, and functional differences (Verbaten, Huyben, & Kemner, 1997). However, because the current research replicated past research, finding P300 to be maximal over central-parietal regions (see Table 1) and not over frontal regions, it can be assumed that the elicited response was a true P300.

The present research suggests that the use of ERP measures may assist in understanding the relationship between emotive individual differences and the processing of affective stimuli. The use of ERPs may provide useful information concerning the timing and neural substrates involved in processing affective stimuli, and may enhance our understanding of the mechanisms underlying normal and abnormal affective processing.

Manuscript received 28 September 2006

Manuscript accepted 25 July 2007

First published online 11 September 2007

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