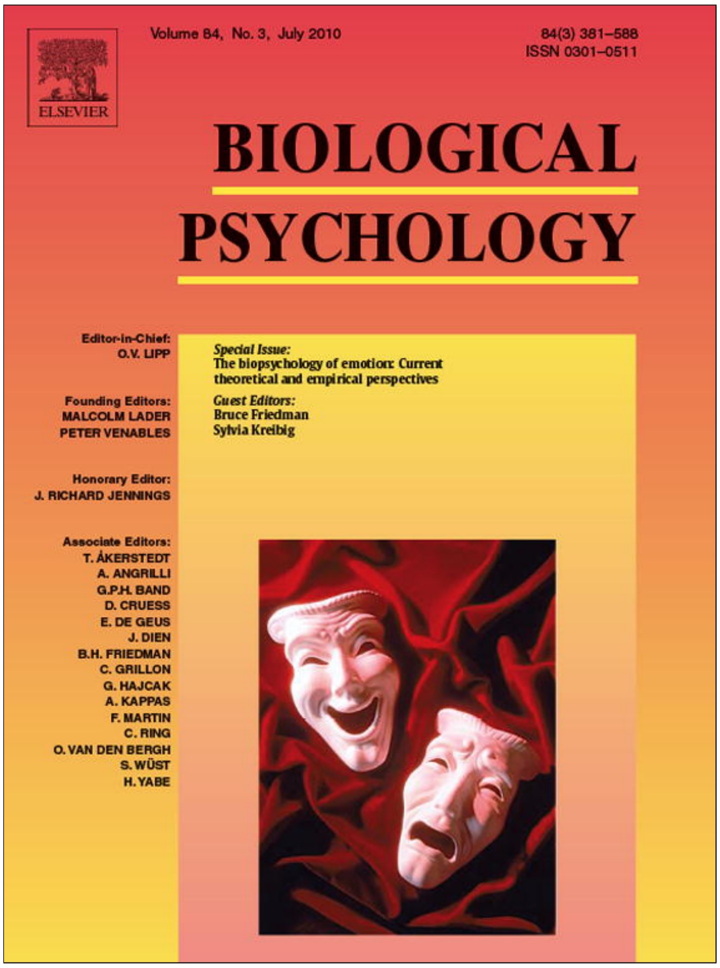
Volume 84, No. 3, July 2010
84(3) 381–588
ISSN 0301-0511
ELSEVIER
BIOLOGICAL
PSYCHOLOGY
Editor-in-Chief:
O.V. LIPP
Founding Editors:
MALCOLM LADER
PETER VENABLES
Honorary Editor:
J. RICHARD JENNINGS
Associate Editors:
T. ÅKERSTEDT
A. ANGRILLI
G.P.H. BAND
D. CRUESS
E. DE GEUS
J. DIEN
B.H. FRIEDMAN
C. GRILLON
G. HAJCAK
A. KAPPAS
F. MARTIN
C. RING
O. VAN DEN BERGH
S. WÜST
H. YABE
Special Issue:
The biopsychology of emotion: Current theoretical and empirical perspectives
Guest Editors:
Bruce Friedman
Sylvia Kreibig

Biological Psychology 84 (2010) 451–462

Contents lists available at ScienceDirect

Biological Psychology

journal homepage: www.elsevier.com/locate/biopsycho

Review

The role of asymmetric frontal cortical activity in emotion-related phenomena: A review and update

Eddie Harmon-Jones *, Philip A. Gable, Carly K. Peterson

Department of Psychology, Texas A&M University, 4235 TAMU, College Station, TX 77845, USA

ARTICLE INFO

Article history:
Received 8 January 2009
Accepted 30 August 2009
Available online 4 September 2009

Keywords:
Cortex
Emotion
Emotional expression
Emotional experience
Cerebral lateralization
Frontal asymmetry
Parietal asymmetry
Approach motivation
Withdrawal motivation
Positive affect
Negative affect

ABSTRACT

Conceptual and empirical approaches to the study of the role of asymmetric frontal cortical activity in emotional processes are reviewed. Although early research suggested that greater left than right frontal cortical activity was associated with positive affect, more recent research, primarily on anger, suggests that greater left than right frontal cortical activity is associated with approach motivation, which can be positive (e.g., enthusiasm) or negative in valence (e.g., anger). In addition to reviewing this research on anger, research on guilt, bipolar disorder, and various types of positive affect is reviewed with relation to their association with asymmetric frontal cortical activity. The reviewed research not only contributes to a more complete understanding of the emotive functions of asymmetric frontal cortical activity, but it also points to the importance of considering motivational direction as separate from affective valence in psychological models of emotional space.

Contents

* Corresponding author.
E-mail address: eddiehj@gmail.com (E. Harmon-Jones).

0301-0511/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.biopsycho.2009.08.010

The role of regional cortical activity, particularly hemispheric lateralization, in emotions has been the subject of interest for several decades. Over the last decade, research on asymmetric frontal cortical activation and emotion has flourished. Consequently, this review will focus primarily on this body of work. Other work on the role of asymmetric parietal cortical activation and emotional processes, though not as extensive, will be reviewed briefly. The review will focus primarily on electroencephalographic (EEG) measures of asymmetric cortical activation because these measures have been used most frequently in examinations of lateralizations of emotional functions.

1. Asymmetric frontal cortical activity and the experience of affective valence

The asymmetric involvement of prefrontal cortical regions in positive affect (or approach motivation) and negative affect (or withdrawal motivation) was suggested over 70 years ago by observations of persons who had suffered damage to the right or left anterior cortex (Goldstein, 1939). Later research supported these observations using the Wada test, which involves injecting amytal, a barbiturate derivative, into one of the internal carotid arteries and suppressing the activity of one hemisphere. Amytal injections in the left side produced depressed affect, whereas injections in the right side produced euphoria (Terzian and Cecotto, 1959; Alema et al., 1961; Perria et al., 1961; Rossi and Rosadini, 1967). These effects were interpreted as reflecting the release of one hemisphere from contralateral inhibitory influences. Thus, activation in the right hemisphere, when not inhibited by the left hemisphere, caused depression; an uninhibited left hemisphere caused euphoria.

Subsequent studies appeared to confirm these results, finding that persons who had suffered left hemisphere damage or lesions tended to show depressive symptoms (Black, 1975; Gasparrini et al., 1978; Gainotti, 1972; Robinson and Price, 1982), whereas persons who had suffered right hemisphere lesions tended to show manic symptoms (Gainotti, 1972; Robinson and Price, 1982; Sackeim et al., 1982). Other research has revealed asymmetries underlying appetitive and avoidant behaviors in non-human animals, in species ranging from great apes and reptiles (Deckel et al., 1998; Hopkins et al., 1993) to chicks (Güntürkün et al., 2000), amphibians (Rogers, 2002), and spiders (Ades and Ramires, 2002).

More recent research suggests that in humans these asymmetric activations are often specific to the frontal cortex. This research often uses asymmetric activation in right versus left frontal cortical areas as a dependent variable, usually assessed by EEG recordings. Frontal cortical asymmetry is assessed by comparing activation levels between comparable areas on the left and right sides. Difference scores are widely used in this research, and their use is consistent with the amytal and lesion research described above that suggests that asymmetry may be the key variable with one hemisphere inhibiting the opposite one. Consistent with that view is evidence from studies of transcranial magnetic stimulation, discussed later in the article (Schutter, 2009; Schutter et al., 2001).

Much of this evidence has been obtained with EEG measures of brain activity, or more specifically, alpha frequency band activity derived from the EEG. Research has revealed that alpha power is inversely related to regional brain activity using hemodynamic measures (Cook et al., 1998) and behavioral tasks (Davidson et al., 1990).

2. Trait affective styles and resting asymmetric frontal activity

In the EEG research, depression has been found to relate to resting frontal asymmetric activity, with depressed individuals showing relatively less left than right frontal brain activity (Jacobs and Snyder, 1996; Schaffer et al., 1983), even when in remission status (Henriques and Davidson, 1990). Other research has revealed that trait positive affect is associated with greater left than right frontal cortical activity, whereas trait negative affect is associated with greater right than left frontal activity (Tomarken et al., 1992). In addition, basal cortisol levels have been found to correlate directly with relatively greater right than left frontal cortical activity (Buss et al., 2003; Kalin et al., 1998; Rilling et al., 2001).

Although there have been several replications of the above effects (e.g., Allen et al., 1993), there have also been failures to replicate (Reid et al., 1998). In response, research has suggested that half of the variance in a resting session is due to trait influences with the remaining half due to state influences (Hagemann et al., 2002, 2005). Thus, the presence of strong and varying situational influence could cause failures to replicate some trait results.

Two situational variables that may influence baseline asymmetric frontal activity are time of day and time of year. Both variables have been found to relate to other measures that are related to asymmetric frontal cortical activity. First, time of year influences basal cortisol and mood. Cortisol levels are highest in fall and winter and lowest in spring (King et al., 2000; Walker et al., 1997). Depressed mood is higher in fall and winter and lower in spring (Nayyar and Cochrane, 1996; Oyane et al., 2008; Partonen and Lonnqvist, 1998). As noted above, greater depression is associated with lesser left frontal activity. Also, greater basal cortisol levels correlate directly with relatively greater right than left frontal cortical activity measured at resting baseline (Buss et al., 2003; Kalin et al., 1998; Rilling et al., 2001). Higher basal cortisol levels have been associated with shyness (Schmidt et al., 1997) and anxious depression (Schulkin et al., 1998). Second, time of day influences basal cortisol levels, with increased levels in the morning, and then decreasing levels throughout the rest of the day, with lowest levels at night (King et al., 2000; Van Cauter, 1989). Also, mood is affected by circadian cycles, so that moods are more negative in the morning and become more positive as the day goes on (Wirz-Justice, 2005).

Because depressed mood and basal cortisol levels correlate with asymmetric frontal cortical activity at baseline, Peterson and Harmon-Jones (2009) predicted that time of day and time of year may be correlated with asymmetric frontal cortical activity. More specifically, relative right frontal activity at resting baseline may be greatest in fall mornings compared to other times. To test this prediction, we simply assessed the relationship between time of day and time of year on resting asymmetric frontal activity. Results of two studies revealed that relative right frontal activity was indeed greatest during fall mornings. Additional analyses suggested that this relationship was not due to subject selection. These results suggest that time of day and time of year may explain why some past studies failed to replicate relationships between frontal asymmetry and other individual difference characteristics. Also, they suggest that these variables be measured and/or controlled in future studies.

Additional, yet-to-be discovered variables may similarly influence resting baseline asymmetric activity. Based on existing evidence (to be reviewed), we would suspect that variables that are associated with state approach/withdrawal motivation would influence resting baseline asymmetric activity. Mood reports may not be sufficiently sensitive to produce relationships with asymmetric frontal cortical activity at rest, however, because past studies have failed to find significant relationships between self-reported mood and resting frontal asymmetry (e.g., for review, see Hagemann, 2004). Along these lines, acute administration of cortisol increases relative right frontal cortical activity, but does not affect self-reported mood (Tops et al., 2005).

2.1. Trait resting asymmetric frontal activity and affective reactions

In addition to the research that suggests that resting baseline frontal asymmetric activity relates to other measures of trait emotion, research has found that resting baseline frontal asymmetric activity predicts emotional responses. For example, individuals with greater right than left frontal activity during baseline recording sessions report larger negative affective responses to negative emotion-inducing films (fear and disgust) and smaller positive affective responses to positive emotion-inducing films (happiness; Tomarken et al., 1990; Wheeler et al., 1993). Also, relative right frontal activity predicts crying in response to maternal separation in 10-month-old infants (Davidson and Fox, 1989).

2.2. Manipulations of asymmetric frontal cortical activity and emotion

2.2.1. Neurofeedback

To test whether these individual differences in asymmetric frontal cortical activity were causally involved in the production of the affective response, research has used neurofeedback training to manipulate asymmetric frontal cortical activity (Allen et al., 2001). Neurofeedback presents the participant with real-time feedback on brainwave activity. If brainwave activity over a particular cortical region changes in the direction desired by the experiment, then the participant is given “reward” feedback; if brainwave activity does not change in the desired direction, either negative feedback or no feedback is given. Rewards can be as simple as the presentation of a tone that informs the participant that brain activity has changed in the desired way. Neurofeedback-induced changes result from operant conditioning, and these changes in EEG can occur without awareness of how the brain activity changes occurred (Kamiya, 1979; Siniatchkin et al., 2000). Participants typically are not aware of how they brought about changes in brain activity; in fact, extensive practice is required to gain awareness of how one may intentionally cause changes in brain activity (e.g., eight weeks of practice, Kotchoubey et al., 2002).

In the experiment, individuals were trained to increase relative right versus relative left frontal activity over several days (Allen et al., 2001). Prior to training, participants were told that neurofeedback training involved using the activity of their brains to cause a computer to generate high or low tones, and that they should try to make the high tone stay on. Participants were not told that the neurofeedback was contingent on asymmetry. The training lasted for 32 min each day. During the first second of each two-second epoch, the difference in alpha power at right and left frontal sites was computed and compared against a criterion value established for that block. If this difference exceeded the criterion value in the desired direction, a 300 Hz reward tone was played; if the criterion was not exceeded, a 150 Hz nonreward tone was played.

Then, on the last day following training, participants were exposed to film clips designed to evoke emotions, and zygomatic (cheek) and corrugator (brow) muscle region activity was recorded. As expected, neurofeedback training altered asymmetric frontal activity, with individuals who received neurofeedback training to increase relative right frontal activity showing a significant change in relative right frontal activity from day 1 to days 3 and 4. Individuals who received training to increase relative left frontal activity did not show a significant change in asymmetric frontal activity, but did differ from the relative right frontal training condition on the latter days. More importantly, this manipulated change in asymmetric frontal cortical activity caused changes in emotional responses, with the increase in right frontal cortical activity condition showing less zygomatic and more corrugator muscle region activity in response to all film clips than the increase left frontal cortical activity condition. This research suggests that asymmetric frontal cortical activity is causally involved in emotional responses.

2.2.2. Hand contractions

Other research has also suggested that asymmetric frontal cortical activity is causally involved in emotional experience. Contractions of the left hand and of the left side of the lower third of the face induce sadness and bias perceptions and judgments negatively, whereas contractions of the right hand and of the right side of the face induce positive affect and assertiveness and bias perceptions and judgments positively (Schiff and Lamon, 1989, 1994).

The effects of contractions of muscles on one side of the body affecting emotional and motivational outcomes have been explained as a result of activation of the contralateral hemisphere. Innervation of facial muscles in the lower third of the face (Rinn, 1984) and of muscles in the hand is contralateral (Hellige, 1993). Thus, it has been assumed that the emotive outcomes produced by the contractions resulted from the spread of activation to, or recruitment of, contralateral frontal areas (Schiff and Lamon, 1989, 1994).

To test these ideas, an experiment was conducted in which participants were randomly assigned to contract their left or right hand by squeezing a ball for roughly four minutes (Harmon-Jones, 2006). Then, participants were exposed to a mildly positive, approach-oriented radio editorial about apartment living options in the city where the participants lived. EEG was recorded followed by completion of an emotion scale that included items designed to measure positive activation (Watson et al., 1999). Results revealed that the unilateral contraction of the hand increased the activation of the contralateral hemisphere, as measured by EEG alpha suppression, over the central and frontal regions. The hand contraction manipulation also affected positive activation, with the right-hand contraction causing greater positive activation than the left-hand contraction. Finally, in the right-hand condition, positive activation was related to greater relative left frontal activity at mid-frontal sites, but not other sites.

2.3. State manipulations of affect and asymmetric frontal cortical responses

Research has also demonstrated that asymmetric frontal brain activity is associated with state emotional responses. For instance, Davidson and Fox (1982) found that 10-month-old infants exhibited increased left frontal activation in response to a film clip of an actress generating a happy facial expression as compared to a sad facial expression. Frontal brain activity has been found to relate to facial expressions of positive and negative emotions, as well. For example, Ekman and Davidson (1993) found increased left frontal activation during voluntary facial expressions of smiles of enjoyment. Coan et al. (2001) found that voluntary facial expressions of fear produced relatively less left frontal activity.

Only a few studies have examined emotional processes and frontal asymmetry using event-related potentials (ERPs). In one study, Cunningham et al. (2005) measured the late positive potential (LPP) while participants made evaluative (good versus bad) and non-evaluative (abstract versus 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 750–1250 ms after event onset) during the viewing of unfamiliar happy faces and larger right frontal ERPs during unfamiliar neutral faces. Similarly, van de Laar et al. (2004) found that cocaine-addicted individuals, but not non-addicted individuals, showed larger positive slow wave responses over the left (but not right) frontal cortex to cocaine-related photographs as compared to neutral photographs. Ohgami et al. (2006) also found ERP evidence that suggested that reward cues caused greater left frontal cortical activity.

Although much research has found asymmetric frontal cortical activations in response to manipulations of emotion, some past research has failed to produce predicted results (see reviews by Murphy et al., 2003; Pizzagalli et al., 2003). One area in which failures to find predicted effects has been especially prevalent is in studies using affective pictures (Elgavish et al., 2003; Hagemann et al., 1998). Affective pictures may not evoke sufficient emotional intensity to engage asymmetric frontal cortical activations for *all* individuals. Moreover, the intermixing of multiple types of affective stimuli may weaken motivational effects (Gable and Harmon-Jones, 2009). To address these issues, Gable and Harmon-Jones (2008) measured individual differences in emotive tendencies toward positive stimuli, and then assessed regional brain activation during viewing of positive stimuli. As predicted, individuals with stronger emotive tendencies (longer time since eaten, more liking for dessert) toward positive stimuli (pictures of desserts) showed greater relative left frontal activation to those stimuli but not to neutral stimuli (see Harmon-Jones and Gable, 2009, for a replication). The affective pictures alone did not cause significant shifts in asymmetric frontal cortical activity.

Taken together, much research has revealed that the left frontal cortical region is involved in the experience of certain positive affects, whereas the right frontal cortical region is involved in the experience of certain negative affects. However, other research, reviewed below, has tested whether the experience of affective valence provides the best explanation of the role of asymmetric frontal cortical activity in emotive processes.

3. Asymmetric frontal cortical activity and the expression of motivational direction

In 1997, two studies observed that trait approach motivation was related to greater left than right frontal activity at resting baseline (Harmon-Jones and Allen, 1997; Sutton and Davidson, 1997). One of these studies found that trait "withdrawal" motivation was related to greater right than left frontal activity at baseline (Sutton and Davidson, 1997), whereas the other found no relationship between trait withdrawal and asymmetric frontal activity (Harmon-Jones and Allen, 1997). Subsequent studies have found trait approach motivation to be associated with greater relative left frontal activity at baseline and found no relationship between trait withdrawal and asymmetric frontal activity, with the measures of trait withdrawal used (Amodio et al., 2008; Coan and Allen, 2003). In all of these studies, motivational direction was measured with the behavioral inhibition/behavioral activation system scales (BIS/BAS) of Carver and White (1994). Sample items from the approach-oriented scale include: "I go out of my way to get things I want"; "I crave excitement and new sensations". Sample items from the withdrawal-oriented scale include: "I worry about making mistakes" and "I have very few fears compared to my friends (reverse scored)." This scale was based on Gray's (1994) theory of motivation. In this theory, BAS is posited to be a motivational system sensitive to signals of conditioned reward, nonpunishment, and escape from punishment. Its activation causes movement toward goals. BIS is hypothesized to be sensitive to signals of conditioned punishment, nonreward, novelty, and innate fear stimuli. It inhibits behavior, increases arousal, prepares for vigorous action, and increases attention toward aversive stimuli.

Other research has conceptually replicated the observation of BIS/BAS and asymmetric frontal cortical activity and extended them by examining the relationship of BIS/BAS with asymmetric frontal cortical responses to affective stimuli (Peterson, Gable, & Harmon-Jones, 2008a). In this study, individuals viewed positive, neutral, and negative affective pictures from the International Affective Picture System (Lang, Bradley, & Cuthbert, 2008). Startle probes (short bursts of white noise) were presented during the midst of picture viewing, and ERPs were measured to the startle probes. Past work by Cuthbert, Schupp, Bradley, McManis, and Lang (1998) found that P300 amplitude at posterior midline sites to the startle probe was reduced during the viewing of pleasant and unpleasant pictures as compared to neutral pictures, regardless of whether participants were instructed to attend to, or ignore, the startle probes. On the other hand, 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) interpreted these results by suggesting 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. The N100, which relates to selective attentional processing, was increased during unpleasant pictures perhaps because early cortical processing is activated by aversive motivation.

Building on these results, we examined whether individual differences in BIS and BAS sensitivity related to these ERP responses to startle probes during affective pictures (Peterson et al., 2008a). More importantly, we tested whether these responses were lateralized over the frontal cortex, with responses involving BAS and positive stimuli being left lateralized and responses involved BIS and negative stimuli being right lateralized. Results replicated the results of Cuthbert et al. (1998) and extended them by revealing that greater BAS scores were associated with smaller left frontal P300 responses during positive pictures, whereas greater BIS scores were associated with larger right frontal N100 responses during negative pictures. These results suggest that BIS sensitivity may be related to relative right frontal cortical activations involved in selective attention toward negative affective stimuli, whereas BAS sensitivity may be related to greater relative left frontal cortical activations involved in working memory processing of positive affective stimuli.

These studies suggested that asymmetric frontal cortical activity could be associated with motivational direction instead of affective valence. However, BIS and BAS are also mostly associated with negative and positive affect, respectively (Carver & White, 1994), and consequently, the interpretation is clouded. Similarly, the finding of promotion (versus prevention) focus being associated with greater relative left (versus right) frontal activation at baseline (Amodio, Shah, Sigelman, Brazy, & Harmon-Jones, 2004) could be interpreted from a motivational direction view or an affective valence view because promotion (versus prevention) is more often associated with positive (versus negative) affect. That is, past research had essentially confounded emotional valence with motivational direction, and researchers were claiming that relatively greater left than right frontal cortical activity reflected greater approach motivation and positive affect, whereas relatively greater right than left frontal cortical activity reflected greater withdrawal motivation and negative affect. These claims fit well into dominant emotion theories that associated positive affect with approach motivation and negative affect with withdrawal motivation (Lang, 1995; Watson, 2000).

However, other theories suggested that approach motivation and positive affect are not always associated with one another. Anger, for example, is a negatively valenced emotion that typically evokes behavioral tendencies of approach (e.g., Darwin, 1872; Ekman & Friesen, 1975; Plutchik, 1980; Young, 1943). Anger is often associated with attack, particularly offensive aggression (e.g., Berkowitz, 1993; Blanchard & Blanchard, 1984; Lagerspetz, 1969). And offensive aggression can be distinguished from defensive aggression, associated with fear. Offensive aggression leads to attack without attempts to escape, whereas defensive or fear-based aggression leads to attack only if escape is not possible.

Other research also suggested that anger was associated with approach motivation (e.g., Izard, 1991; Lewis, Alessandri, & Sullivan, 1990; Lewis, Sullivan, Ramsay, & Alessandri, 1992). More recent studies examined whether trait behavioral approach or BAS was associated with anger-related responses. Several studies have found that trait BAS, as assessed by Carver and White's (1994) scale, is positively related to trait anger at the simple correlation level (Harmon-Jones, 2003; Smits & Kuppens, 2005). Carver (2004) also found that trait BAS predicts state anger in response to situational anger manipulations. BAS sensitivity has been found to predict aggressive inclinations even more strongly when approach motivation was first primed (Harmon-Jones & Peterson, 2008). In addition, BAS predicted vigilance to angry faces presented out of awareness, consistent with the idea that attention toward angry faces is the first step in an approach-based dominance confrontation (Putman et al., 2004). In contrast, individuals with greater social anxiety show more avoidance-related attention toward angry faces (Putman et al., 2004).[1]

Because of the large body of evidence suggesting that anger is often associated with approach motivation (see Carver and Harmon-Jones, 2009, for a review), research has been conducted to examine the relationship between anger and relative left frontal activation to test whether asymmetric frontal cortical activity is due to emotional valence, motivational direction, or a combination of emotional valence and motivational direction.

3.1. Asymmetric frontal cortical activity and anger

Because anger is typically associated with approach motivation, assessing the relationship of anger and asymmetric frontal cortical activity can assist in determining whether asymmetric frontal cortical activity relates to motivational direction or affective valence. If asymmetric frontal cortical activity relates to motivational direction, then anger should relate to greater left than right frontal activity, because anger is associated with approach motivational direction. However, if asymmetric frontal cortical activity relates to affective valence, then anger should relate to greater right than left frontal activity, because anger is associated with negative valence.

[1] The results of Putman et al. (2004) appear to contradict the previously reviewed results by Peterson et al. (2008a,b) that found that BIS predicted greater right frontal N1 amplitudes to startle probes presented during negative IAPS pictures. Putman et al. examined behavioral responses in an emotional facial expression Stroop-type task, whereas Peterson et al. examined ERPs to startle probes during IAPS pictures. These methodological differences (e.g., behavior versus ERP) may be responsible for the apparent contradiction in results. Also, different aspects of attention may be assessed by these different methods.

3.1.1. Trait anger

In a study testing these competing predictions, Harmon-Jones and Allen (1998) assessed trait anger using the aggression questionnaire by Buss and Perry (1992) and assessed asymmetric frontal activity by examining baseline, resting EEG activity. In this study of adolescents, trait anger related to increased left frontal activity and decreased right frontal activity. Asymmetric activity in other regions did not relate with trait anger. The specificity of anger to frontal asymmetries and not other region asymmetries has been observed in all of the reviewed studies on anger.

Other research addressed an alternative explanation for the observation that relative left frontal activity related to anger (Harmon-Jones, 2004). The alternative explanation suggested that persons with high levels of trait anger might experience anger as a positive emotion, and this positive feeling or attitude toward anger could be responsible for anger being associated with relative left frontal activity. After developing a valid and reliable assessment of attitude toward anger, a study was conducted to assess whether resting baseline asymmetric activity related to trait anger and attitude toward anger. Results indicated that trait anger related to relative left frontal activity and not attitude toward anger, and regression analyses revealed that the relationship between trait anger and left frontal activity was not due to positive attitudes toward anger.

3.1.2. State anger

To address the limitations inherent in correlational studies, experiments were conducted in which anger was manipulated. Harmon-Jones and Sigelman (2001) found that individuals who were insulted evidenced greater relative left frontal activity than individuals who were not insulted. Additional analyses revealed that within the insult condition, reported anger and aggression were positively correlated with relative left frontal activity. Neither of these correlations was significant in the no-insult condition. Harmon-Jones et al. (2009) conceptually replicated the above research and extended it by showing that social rejection causes increased relative left frontal activity that is associated with anger and jealousy. Jensen-Campbell et al. (2007) and Verona et al. (2009) also replicated Harmon-Jones and Sigelman's (2001) results, with the latter group extending them by showing that an impersonal stressor (high pressure air blasts assigned by a computer) also evokes greater relative left frontal activity, which correlates with aggression in an "employee–supervisor" lab task.

Other work replicated these results and revealed that state anger evokes both increased left and decreased right frontal activity. In the same experiment, when participants were first induced to feel sympathy for a person who insulted them, this reduced the effects of insult on left and right frontal activity (Harmon-Jones et al., 2004), consistent with the idea that sympathy reduces aggression (Miller and Eisenberg, 1988).

3.1.3. Independent manipulation of approach motivation within anger

In the experiments just described, the designs were tailored in such a way as to evoke anger that was approach oriented. Although most instances of anger involve approach inclinations, it is possible that not all forms of anger are associated with approach motivation. To manipulate approach motivation independently of anger, Harmon-Jones et al. (2003) performed an experiment in which the ability to cope with the anger-producing event was manipulated. Based on past research that has revealed that coping potential affects motivational intensity (Brehm, 1999; Brehm and Self, 1989), it was predicted that the expectation of being able to take action to resolve the anger-producing event would increase approach motivational intensity relative to expecting to be unable to take action. In support of this prediction, angered participants who expected to engage in approach-related action evidenced greater left frontal activity than angered participants who expected to be unable to engage in approach-related action. Moreover, within only the action-possible condition, participants who evidenced greater left frontal activity in response to the angering event also evidenced greater self-reported anger and engaged in more approach-related behavior.

The research of Harmon-Jones et al. (2003) suggests that the left frontal region is most accurately described as a region sensitive to approach motivational intensity. That is, it was only when anger was associated with an opportunity to behave in a manner to resolve the anger-producing event that participants evidenced the increased relative left frontal activation.

The effect of approach motivation and anger on left frontal activity has also been produced using pictorial stimuli that evoke anger (Harmon-Jones et al., 2006). In this experiment, participants low in racial prejudice were shown neutral, positive, and fear/disgust pictures from the International Affective Picture System (Lang et al., 2008). Mixed among those pictures were pictures depicting instances of racism and hatred (e.g., neo-Nazis, Ku Klux Klan). Prior to viewing the pictures, half of the participants were informed that they would write an essay on why racism is immoral, unjust, and unfair at the end of the experiment. This manipulation served to increase their anger-related approach motivation. Results revealed that participants showed greater relative left frontal activity to anger pictures than other picture types only when they expected to engage in approach-related behavior. A second study revealed that individuals who scored lower in racial prejudice evidenced even greater relative left frontal activation to the anger-evoking racist pictures in the approach motivation condition (Harmon-Jones et al., 2006, Study 2).

The above findings may suggest that relatively greater left frontal activity will occur in response to an angering situation only when there is an explicit approach motivational opportunity. However, it is possible that an explicit approach motivational opportunity is not necessary for increased left frontal activity to anger to occur, but that it only intensifies left frontal activity. In other words, other features of the situation or person may make it likely that an angering situation will increase approach motivational tendencies and activity in the left frontal cortical region. For example, individuals who are chronically high in anger may evidence increased left frontal activity (and approach motivational tendencies) in response to angering situations that would not necessarily cause such responses in individuals who are not as angry. This prediction is predicated on the idea that individuals high in trait anger have more extensive associative networks of anger experience than individuals with lower trait anger, and that anger-evoking stimuli should therefore activate parts of the network more readily in individuals high in trait anger (Berkowitz, 1993; Berkowitz and Harmon-Jones, 2004).

In the study, participants were exposed to anger-inducing pictures (and other pictures) and given no explicit manipulations of action expectancy (Harmon-Jones, 2007). Across all participants, a null effect of relative left frontal asymmetry occurred. However, individual differences in trait anger related to relative left frontal activity to the anger-inducing pictures, such that individuals high in trait anger showed greater left frontal activity to anger-producing pictures (controlling for activity to neutral pictures). These results suggest that the explicit manipulation or opportunity for approach motivated action may potentiate the effects of approach motivation on relative left frontal activity, but may not be necessary.

Additional support for the role of approach motivational intensity being involved in the anger and frontal asymmetry relationship comes from a recent experiment in which body posture was manipulated to influence approach motivational intensity (Harmon-Jones and Peterson, in press). Past research has suggested that manipulated body postures can affect behavior, with slumped postures leading to more "helpless behaviors" (Riskind and Gotay, 1982). Similarly, lying flat on one's back may be antithetical to approach motivation, or the urge to move toward something. In the experiment, participants were randomly assigned to an upright or reclined body position, and then they received neutral or insulting interpersonal feedback, as in previous research (Harmon-Jones et al., 2004). For participants who received the feedback while upright, results replicated past research, with the insulting feedback causing greater relative left frontal activation than the neutral feedback. In contrast, participants who were insulted while in a reclined position did not show the typical increase in relative left frontal activation. This research further supports the role of approach motivation in the anger-relative left frontal activity relationship. Moreover, it has implications not only for the study of embodiment but also for the study of neural processes, because some neuroscience techniques (e.g., fMRI) rely on individuals being in supine positions.

3.1.4. Manipulation of frontal cortical activity and anger processing

Other research is consistent with the hypothesis that anger is associated with left frontal activity. For example, d'Alfonso et al. (2000) used slow repetitive transcranial magnetic stimulation (rTMS) to inhibit the left or right prefrontal cortex. Slow rTMS produces inhibition of cortical excitability, so that rTMS applied to the right prefrontal cortex decreases its activation and causes the left prefrontal cortex to become more active, while rTMS applied to the left prefrontal cortex causes activation of the right prefrontal cortex. They found that rTMS applied to the right prefrontal cortex caused selective attention towards angry faces, whereas rTMS applied to the left prefrontal cortex caused selective attention away from angry faces. Thus, an increase in left prefrontal activity led participants to attentionally approach angry faces, as in an aggressive confrontation. In contrast, an increase in right prefrontal activity led participants to attentionally avoid angry faces, as in a fear-based avoidance. Conceptually similar results have been found by van Honk and Schutter (2006). The interpretation of these results concurs with other research demonstrating that attention toward angry faces is associated with high levels of self-reported anger and that attention away from angry faces is associated with high levels of cortisol (van Honk et al., 2001, 1998, 1999), which is associated with fear.

We recently extended the work of van Honk, Schutter, and colleagues by examining whether a manipulation of asymmetric frontal cortical activity would affect behavioral aggression. Based on past research showing that contraction of the left hand increases right frontal cortical activity and that contraction of the right hand increases left frontal cortical activity (Harmon-Jones, 2006), we manipulated asymmetric frontal cortical activity by having participants contract their right or left hand. Participants then received insulting feedback ostensibly from another participant. They then played a reaction time game on the computer against the other ostensible participant (so that aggression could be measured). Participants were told they could give the other participant a blast of 60–100 dB of white noise for up to 10 s if they were fastest to press the shift key when an image appeared on the screen. Results indicated that participants who squeezed with their right hand gave significantly louder and longer noise blasts to the other ostensible participant than those who squeezed with their left hand (Peterson et al., 2008b). Also, within the right-hand contraction condition, greater relative left frontal activation was correlated with more aggression.

3.1.5. Anger and withdrawal motivation

The reviewed research suggests that greater relative left frontal activation is associated with anger because anger is often associated with approach motivation. This conclusion is most strongly supported in the studies by Harmon-Jones et al. (2003, 2006) that showed that reducing the approach motivational intensity of anger reduces relative left frontal activation.

Is it possible for anger to be associated with an increase in right frontal activation? Based on the motivational direction model, we would expect that anger may be associated with right frontal activation if the anger evoked withdrawal motivational tendencies. However, anger may be evolutionarily prepared to evoke approach motivation, and it thus may be difficult for anger to activate withdrawal motivation. Indeed, research with infants (Lewis et al., 1992) and non-human animals (Blanchard and Blanchard, 1984) suggests that anger is predominantly associated with approach motivational tendencies.

Wacker et al. (2003) designed an experiment to test whether anger associated with withdrawal motivation would cause greater relative right frontal activation. In their experiment, soccer players were instructed to imagine that they were unfairly prevented from playing a soccer game by the coach. In the anger-approach condition, participants imagined approaching the coach and protesting, whereas in the anger-withdrawal condition, they imagined backing out of the locker room and swearing silently at the coach. Results revealed that while both conditions evoked self-reported anger, they did not differ from one another in relative left frontal activation.

Another study by Hewig et al. (2004) assessed the relationship between resting baseline frontal asymmetry and trait anger-out, trait anger-in, and trait anger-control, using the trait scales of the State-Trait Anger Expression Questionnaire (Spielberger, 1988). Anger-out is characterized as "expressing angry feelings in aggressive verbal or motor behavior directed toward other people or objects in the environment" (e.g., "When angry or furious, I lose my temper"; Spielberger et al., 1995, p. 57). Thus, anger-out may be considered an approach-related facet of anger expression. Anger-in measures the degree to which the respondent holds anger in (e.g., "When angry or furious, I keep things in"); and anger-control measures the degree to which the respondent controls anger (e.g., "When angry or furious, I control my angry feelings."). Results revealed that whereas trait anger-out was associated with greater relative left frontal activity at resting baseline, trait anger-control was associated with greater relative right frontal activity. Trait anger-in was not associated with resting frontal asymmetry. Hewig et al. suggested that anger-control related to relative right frontal activity because anger-control is associated with withdrawal motivation.

The idea that anger can be associated with withdrawal motivational tendencies has some intuitive appeal (reviewers of our past anger research have suggested this as a possibility), but the evidence just reviewed provides mixed support for the idea. It is possible that anger may be associated with withdrawal motivation when the angering situation also evokes punishment concerns. If the expression of anger is perceived to be socially inappropriate, some individuals may withdraw from the context rather than evidence approach-oriented anger.

To test these ideas, Zinner et al. (2008) created a social context in which the experience of anger was considered socially inappropriate. Given the norms encouraging political correctness and discouraging public expressions of racial prejudice (Plant and Devine, 1998), some individuals may become angered by the pressure to behave in a politically correct (PC) manner but also want to avoid expressing anger, leading them to withdraw. Along these lines, past research found that some people feel anger when required to comply with social pressure to respond without racial prejudice (Plant and Devine, 2001).

In the Zinner et al. (2008) study, White participants were led to believe they were going to interact with a Black participant (as in Plant and Devine, 2003). To increase the likelihood that some participants would experience anger, the study rationale heightened PC pressure by emphasizing the importance of harmonious interracial interactions. After learning they were going to interact with a Black person, participants' frontal cortical activity was assessed as they "mentally prepared" for the interaction. Immediately before the interaction was about to take place, participants reported their affect about the upcoming interaction. Results revealed that self-reported anger was related to greater relative right frontal cortical activity. Anger was also associated with increased skin conductance levels suggesting that individuals who felt angry were more aroused. Moreover, anger was associated with more spontaneous eye blinking, which has been linked to emotion suppression efforts (Gross and Levenson, 1993). Perhaps participants tried to suppress their negative feelings because of concerns of being socially inappropriate. Finally, anger was associated with anxiety suggesting that this situation had evoked concerns of punishment among individuals who became angry. These results support the idea that anger was associated with relative right frontal activation because of withdrawal motivation.

3.1.6. Bipolar disorder

Research on asymmetric frontal cortical activity and its relationship to motivational direction has been extended to assist in testing a theory concerned with the causes and consequences of bipolar disorder. According to this theory, bipolar individuals demonstrate an excessive increase in approach motivation in response to rewards, goal striving, and anger evocation and an excessive decrease in approach in response to events such as definite failure. Excessive approach motivation is predicted to be reflected in hypomanic and manic symptoms. Several results are consistent with this hypothesis. Compared with control groups, individuals with bipolar I disorder (Meyer et al., 2001) and individuals prone to hypomanic symptoms (Meyer et al., 1999) show elevated scores on self-report measures of BAS sensitivity (Carver and White, 1994), activation (subscale from Internal State Scale; Bauer et al., 1991), and achievement motivation (Johnson et al., 2005). Also, goal-striving (Nusslock et al., 2007) and goal-attainment (Johnson et al., 2000) life events have been associated with an increase in hypomanic/manic, but not depressive, episodes. According to this BAS theory of bipolar disorder, if an event is perceived as a "challenge" and elicits approach-motivated perceptions of successful coping, the BAS should be activated and hypomania/mania symptoms may ensue.

Consistent with this theory and with work on asymmetric frontal cortical activity, increased relative right frontal activity, as measured in EEG resting baseline measurements, has been observed in bipolar depression (Allen et al., 1993), whereas increased relative left frontal activity has been observed in mania (Kano et al., 1992). Also, proneness to hypomania/mania symptoms is related to increased relative left frontal cortical activity in response to anger-evoking events (Harmon-Jones et al., 2002).

A recent study examined whether bipolar spectrum individuals would evidence exaggerated approach motivational tendencies in response to an event that should activate the BAS—goal-striving (Harmon-Jones et al., 2008a). Specifically, bipolar spectrum individuals and non-bipolar individuals participated in a study in which relative left frontal cortical activity was assessed as individuals prepared to solve tasks that varied in difficulty (i.e., easy, medium, and hard) and whether a potential reward or punishment was expected (i.e., individuals could gain or avoid losing money on each trial). Because individuals with bipolar disorder show heightened BAS sensitivity and achievement motivation, it was predicted that relative left frontal activation differences between bipolar and non-bipolar participants would be most likely to occur to hard tasks because bipolar individuals may be especially responsive to such a challenge. This prediction follows from motivational theory (Brehm and Self, 1989; Wright et al., 1995) that predicts that (non-bipolar) individuals should motivationally disengage when the task becomes more difficult than the effort or outcome is worth. Bipolar individuals, on the other hand, were predicted to not show this adaptive, energy conserving response but continue to be motivated even when confronted with very difficult or impossible tasks. In addition, it was predicted that bipolar participants would be even more reactive to the reward (gain) condition, especially when it is hard. This prediction was predicated on past research that suggests that bipolar individuals are especially sensitive to reward and research that suggests that punishment cues often evoke both BIS and BAS activation. In line with predictions, bipolar individuals, as compared to non-bipolar individuals, exhibited greater relative left frontal cortical activation to the hard/rewarding task. Also, among bipolar individuals, current self-reported hypomanic state predicted increased left frontal activation to the tasks. This suggests that the effect of the bipolar diagnosis on left frontal activation to the challenging goal-striving task was partly driven by current hypomanic state at the time of recording. This study highlights the importance of integrating research and theory on biological and psychosocial models of bipolar disorder. Moreover, the research provides important clinical support for the motivational direction model of asymmetric frontal cortical activity.

3.1.7. Guilt

Research on asymmetric frontal cortical activity has been extended into the study of guilt to better understand the motivational functions of guilt. In addition, this study delved into a previously unaddressed but important issue in research on asymmetric frontal cortical activity: Does asymmetric frontal cortical activity fluctuate in response to changes in motivational intensity over relatively brief periods of time? If asymmetric frontal cortical activity is indeed tracking approach motivation, it should change as approach motivational intensity changes. Guilt provided an excellent opportunity to test these ideas because guilt is hypothesized to serve two functions that operate in temporal sequence (Amodio et al., 2007). Guilt first causes a reduction in approach motivation once one becomes aware of having committed a social transgression. This reaction is followed by an increase in approach motivation when one is presented with an opportunity to engage in behavior to repair the transgression.

To test these hypotheses, White Americans low in racial prejudice were given feedback that indicated they had just shown evidence of prejudice toward Blacks while viewing pictures of Blacks, Whites, and Asians. Immediately following the presentation of this feedback, EEG was recorded for 2 min and self-reported emotions were measured. Then, participants' motivational and behavioral responses to stimuli associated with reparation (e.g., prejudice reduction) were measured. This was accomplished by presenting magazine article titles that were relevant (e.g., "10 ways to reduce prejudice in everyday life") or irrelevant to reparation (e.g., "Five steps to a healthier lifestyle"). After each title was presented, participants rated the extent to which they would want to read the article.

Consistent with hypotheses, guilt was initially associated with decreased relative left frontal activation, suggesting a decrease in approach motivation. In contrast, when participants were given the opportunity for reparation, their feelings of guilt predicted interest in prejudice-reducing behavior, which in turn was accompanied by greater relative left frontal activity. These results suggest that asymmetric frontal cortical activity fluctuates with changes in approach motivation even when these changes occur over relatively short periods of time.

3.2. Asymmetric frontal activity and low versus high approach motivated positive affect

The separation of emotional valence from motivational direction suggests that positive affects vary in motivational intensity. That is, some positive affects are lower in approach motivation, whereas others are higher in approach motivation. An important question remains regarding the valence versus motivational direction models of asymmetric frontal cortical activity: Do positive affects of any approach motivational intensity cause increases in relative left frontal activation? An experiment addressed this question by assigning participants to write a short essay on one of three topics (Harmon-Jones et al., 2008b). In the *neutral mindset* condition, participants wrote about an ordinary and neutral day in their life. In the *high-approach-positive mindset* condition, participants wrote about a goal that they intend to accomplish within the next 3 months. In the *low-approach-positive mindset* condition, participants wrote about a time when something exceptionally positive happened to them that did not result from something they did (e.g., when someone did something wonderful for them). After writing about the event, participants were instructed to think about the event while EEG was recorded. Consistent with predictions, participants in the two positive mindset conditions reported feeling more positive affect than participants in the neutral mindset condition. More importantly, the high-approach-positive mindset condition caused greater relative left frontal cortical activity than the other conditions. These results support the hypothesis that it is the approach motivational aspect of some forms of positive affect, and not the positive valence per se, that causes greater relative left frontal cortical activation (as measured by EEG).

4. Other measures and cortical regions

4.1. Other neural measures

The reviewed research strongly suggests that greater relative left frontal cortical activity is associated with approach motivation. However, several important questions remain. For instance, EEG methods utilized in most of this past research do not provide precise information regarding which specific areas of the left frontal cortex are involved in approach motivation. Source localization of EEG alpha power suggests that the left dorsolateral prefrontal cortex is involved (Pizzagalli et al., 2005). But more EEG studies utilizing source localization methods are needed in the frontal asymmetry literature.

Studies measuring hemodynamic responses (fMRI/PET) have produced mixed support for the role of asymmetric dorsolateral prefrontal cortical activity as being associated with approach motivation (Murphy et al., 2003; Wager et al., 2003 but see Berkman & Lieberman, in press). This mixed support may be due to a number of factors. First, fMRI and PET require a supine body position. Research shows that this body position itself reduces relative left frontal activation to anger-inducing insults (Harmon-Jones and Peterson, in press). This finding is consistent with an embodiment hypothesis that lying on one's back is antithetical to approach-oriented behavior, particularly aggression.

Second, EEG and fMRI/PET may assess different populations of neurons. EEG signals result from very selective areas of current source activity, often corresponding to small subsets of total synaptic action in tissue volumes and largely independent of action potentials. PET/fMRI measures, in contrast, result from activity in areas requiring much hemodynamic/metabolic activity. For example, cortical stellate cells occupy roughly spherical volumes and their synaptic sources provide a "closed field" structure, which make them invisible to EEG. Although stellate cells constitute only about 15% of the neural population of the neocortex (Braitenberg and Schuz, 1991; Wilson et al., 1994), they contribute disproportionately to cortical metabolic activity (Connors and Gutnick, 1990). Thus, they have a large effect on fMRI and PET. Other cases yield strong EEG signals and weak fMRI/PET activity. EEG can be large when only a few percent of neurons in each cortical column are "synchronously active," if a large-scale synchrony among different columns produces a large dipole in which individual columns tend to be phase locked in particular frequencies. In this case, because most neurons in each intra-column population are relatively inactive, there is minimal metabolic activity.

EEG does not provide the spatial resolution of fMRI/PET. But that does not eliminate EEG as a useful tool. The observation of frontal hemispheric asymmetries has shed light on important issues in the study of emotion, motivation, and associated clinical problems. Moreover, as reviewed, the EEG findings converge with results from lesion and rTMS studies.

Further research is needed to examine how EEG and fMRI research on asymmetric frontal cortical activity may contribute to each other. For example, combining the fMRI and EEG methods may allow more precise spatial localization of cortical and subcortical structures that contribute to the observed EEG asymmetry. Inclusion of PET with EEG may also permit discovery of neurotransmitters involved in EEG asymmetry and emotion relationships.

4.2. Other cortical regions

The reviewed studies suggest that motivational processes are asymmetrically organized in frontal regions but not other cortical regions. However, some research has suggested that posterior cortical regions are asymmetrically involved in emotional perception (e.g., Borod et al., 1998). That is, the perception of affect, regardless of its valence or motivational direction, has been posited to be processed in right posterior regions (Davidson, 1984). Early research testing this hypothesis found that greater relative right parietal activation, as measured by alpha power, occurred in both adults and children during viewing of both negative and positive stimuli (Davidson et al., 1979; Davidson and Fox, 1982). More recent studies have found that both positive and negative emotionally arousing stimuli produce larger LPPs, N2s, P2s, and early P3s in the right parietal region (Kayser et al., 1997, 2000; Keil et al., 2001; Thomas et al., 2007). These effects have been found using affective pictures and words, and the use of these different types of stimuli as well as different processing tasks (e.g., during midst of Stroop task versus not) may explain why different ERP components are affected in different studies.

Additional research has supported the involvement of the right posterior regions in emotional perception. Patients with lesions to right posterior regions show difficulty recognizing facial expressions (e.g. Bowers and Heilman, 1984; Bowers et al., 1985), although there is evidence that lesions anywhere in the right hemisphere can cause problems with perception of emotional expressions (e.g. Kolb and Taylor, 1991). Furthermore, activation of the right temporoparietal cortex during the perception of emotional facial expressions has been seen using PET imaging (Gur et al., 1994). Taken together, the extant evidence suggests that parietal asymmetries are associated with emotional perception, whereas frontal asymmetries are associated with motivational direction.

5. Summary and conclusion

Much research has supported the thesis that greater left as compared to right frontal activity is associated with approach motivational processes. Other research has suggested that greater right as compared to left frontal activity is associated with withdrawal motivational processes. However, the research testing the withdrawal-right-frontal-region part of the motivational direction model is not as extensive as the research testing the approach-left-frontal-region portion of the model. More experiments that manipulate withdrawal are needed. These experiments may be challenging, however, because of the empirical difficulty of separating purely withdrawal processes from active avoidance processes. Separating withdrawal from active avoidance is vital because active avoidance may engage the approach motivation system (Gray, 1994). Also needed are studies that separate withdrawal from inhibition, as some studies have suggested that regions of right prefrontal cortex are involved in inhibition (Aron et al., 2004; Knoch et al., 2006). Future research is also needed to explore whether specific aspects of approach motivation (e.g., response preparation; attention or reactivity to appetitive stimuli; maintenance of motivational set) are more likely implemented by the left frontal cortical region. Also, work is needed to understand precisely which sub-regions of the left frontal cortex are involved in approach motivational processes. Some research has suggested involvement of the dorsolateral prefrontal cortex but more research is necessary.

In addition to leading to a better understanding of the involvement of asymmetric frontal cortical activity in emotive processes, the reviewed research has also made contributions to emotion theories. By exploring the cortical regions underlying emotion processes, the research has suggested the importance of delineating emotional experience from emotional expression and emotional valence from motivational intensity and direction. Moreover, the reviewed research contributes to the conceptualization of emotional space. Whereas previous research and theory have emphasized emotional valence and arousal as primary dimensions underlying emotions (Lang, 1995; Watson, 2000), and even suggested that valence is directly related to motivational direction, the research reviewed herein suggested a more nuanced view. It suggests that the valence of the emotion may be separable from the motivational direction of the emotion, so that negatively valenced emotions such as anger can be approach motivating. The addition of an independent dimension of motivational direction or some other conceptual arrangement (Carver and Harmon-Jones, 2009) appears to be necessary to accommodate all the data. In the end, the reviewed research highlights the value of affective neuroscience to the development and modification of theories concerned with the psychology of emotion.

Acknowledgements

Work on this article was supported by National Science Foundation grants BCS 0350435 and BCS 0643348.

References

Ades, C., Ramires, E.N., 2002. Asymmetry of leg use during prey handling in the spider *Scytodes globula* (Scytodidae). Journal of Insect Behavior 15, 563–570.

Alema, G., Rosadini, G., Rossi, G.F., 1961. Preliminary experiments on the effects of the intracarotid introduction of sodium amytal in Parkinsonian syndromes. Bollettino della Società italiana di biologia sperimentale 37, 1036–1037.

Allen, J.J.B., Harmon-Jones, E., Cavender, J.H., 2001. Manipulation of frontal EEG asymmetry through biofeedback alters self-reported emotional responses and facial EMG. Psychophysiology 38, 685–693.

Allen, J.J.B., Iacono, W.G., Depue, R.A., Arbisi, P., 1993. Regional electroencephalographic asymmetries in bipolar seasonal affective disorder before and after exposure to bright light. Biological Psychiatry 33, 642–646.

Amodio, D.M., Devine, P.G., Harmon-Jones, E., 2007. A dynamic model of guilt: implications for motivation and self-regulation in the context of prejudice. Psychological Science 18, 524–530.

Amodio, D.M., Master, S.L., Yee, C.M., Taylor, S.E., 2008. Neurocognitive components of behavioral inhibition and activation systems: implications for theories of self-regulation. Psychophysiology 45, 11–19.

Amodio, D.M., Shah, J.Y., Sigelman, J., Brazy, P.C., Harmon-Jones, E., 2004. Implicit regulatory focus associated with resting frontal cortical asymmetry. Journal of Experimental Social Psychology 40, 225–232.

Aron, A.R., Robbins, T.W., Poldrack, R.A., 2004. Inhibition and the right inferior frontal cortex. Trends in Cognitive Sciences 8, 170–177.

Bauer, M.S., Crits-Christoph, P., Ball, W.A., Dewees, E., McAllister, T., Alahi, P., Cacciola, J., Whybrow, P.C., 1991. Independent assessment of manic and depressive symptoms by self-rating: scale characteristics and implications for the study of mania. Archives of General Psychiatry 48, 807–812.

Berkman, E. T., Lieberman, M. D., in press. Approaching the good and avoiding the bad: Separating action and valence using dorsolateral prefrontal cortical asymmetry. Journal of Cognitive Neuroscience.

Berkowitz, L., 1993. Aggression: Its Causes, Consequences, and Control. McGraw-Hill, New York.

Berkowitz, L., Harmon-Jones, E., 2004. Toward an understanding of the determinants of anger. Emotion 4, 107–130.

Black, E.W., 1975. Unilateral brain lesions and MMPI performance: a preliminary study. Perceptual and Motor Skills 40, 87–93.

Blanchard, R.J., Blanchard, D.C., 1984. Affect and aggression: an animal model applied to human behavior. In: Blanchard, R.J., Blanchard, D.C. (Eds.), Advances in the Study of Aggression. Academic Press, Orlando, pp. 1–62.

Borod, J.C., Bloom, R.L., Haywood, C.S., 1998. Verbal aspects of emotional communication. In: Beeman, M., Chiarello, C. (Eds.), Right Hemisphere Language Comprehension: Perspectives in Cognitive Neuroscience. Lawrence Erlbaum, Mahwah, NJ, pp. 285–307.

Bowers, D., Bauer, R.M., Coslett, H.B., Heilman, K.M., 1985. Processing of faces by patients with unilateral hemisphere lesions. Brain Cognition 4, 258–272.

Bowers, D., Heilman, K.M., 1984. Dissociation between the processing of affective and nonaffective faces: a case study. Journal of Clinical and Experimental Neuropsychology 6, 367–379.

Braitenberg, V., Schuz, A., 1991. Anatomy of the Cortex: Statistics and Geometry. Springer-Verlag.

Brehm, J.W., 1999. The intensity of emotion. Personality and Social Psychology Review 3, 2–22.

Brehm, J.W., Self, E.A., 1989. The intensity of motivation. Annual Review of Psychology 40, 109–131.

Buss, A.H., Perry, M., 1992. The aggression questionnaire. Journal of Personality and Social Psychology 63, 452–459.

Buss, K., Malmstadt Schumacher, J.R., Dolski, I., Kalin, N.H., Goldsmith, H.H., Davidson, R.J., 2003. Right frontal brain activity, cortisol, and withdrawal behavior in 6-month-old infants. Behavioral Neuroscience 117, 11–20.

Carver, C.S., 2004. Negative affects deriving from the behavioral approach system. Emotion 4, 3–22.

Carver, C.S., Harmon-Jones, E., 2009. Anger is an approach-related affect: evidence and implications. Psychological Bulletin 135, 183–204.

Carver, C.S., White, T.L., 1994. Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: The BIS/BAS scales. Journal of Personality and Social Psychology 67, 319–333.

Coan, J.A., Allen, J.J.B., Harmon-Jones, E., 2001. Voluntary facial expression and hemispheric asymmetry over the frontal cortex. Psychophysiology 38, 912–925.

Coan, J.A., Allen, J.J.B., 2003. Frontal EEG asymmetry and the behavioral activation and inhibition systems. Psychophysiology 40, 106–114.

Connors, B.W., Gutnick, M.J., 1990. Intrinsic firing patterns of diverse neocortical neurons. Trends in Neuroscience 13, 99–104.

Cook, I.A., O'Hara, R., Uijtdehaage, S.H.J., Mandelkern, M., Leuchter, A.F., 1998. Assessing the accuracy of topographic EEG mapping for determining local brain function. Electroencephalography and Clinical Neurophysiology 107, 408–414.

Cunningham, W.A., Espinet, S.D., DeYoung, C.G., Zelazo, P.D., 2005. Attitudes to the right and left: Frontal ERP asymmetries associated with stimulus valence and processing goals. NeuroImage 28, 827–834.

Cuthbert, B.N., Schupp, H.T., Bradley, M., McManis, M., Lang, P.J., 1998. Probing affective pictures: attended startle and tone probes. Psychophysiology 35, 344–347.

d'Alfonso, A.A.L., van Honk, J., Hermans, E., Postma, A., de Haan, E.H.F., 2000. Laterality effects in selective attention to threat after repetitive transcranial magnetic stimulation at the prefrontal cortex in female subjects. Neuroscience Letters 280, 195–198.

Darwin, C., 1872/1965. The Expressions of the Emotions in Man and Animals. Oxford University Press, New York, NY.

Davidson, R.J., 1984. Hemispheric asymmetry and emotion. In: Scherer, K., Ekman, P. (Eds.), Approaches to Emotion. Erlbaum, Hillsdale, NJ, pp. 39–57.

Davidson, R.J., Chapman, J.P., Chapman, L.J., Henriques, J.B., 1990. Asymmetric brain electrical-activity discriminates between psychometrically-matched verbal and spatial cognitive tasks. Psychophysiology 27, 528–543.

Davidson, R.J., Fox, N., 1982. Asymmetric brain activity discriminates between positive and negative affective stimuli in 10 month old infants. Science 218, 1235–1237.

Davidson, R.J., Fox, N.A., 1989. Frontal brain asymmetry predicts infants' response to maternal separation. Journal of Abnormal Psychology 98, 127–131.

Davidson, R.J., Schwartz, G.E., Saron, C., Bennett, J., Goleman, D., 1979. Frontal versus parietal EEG asymmetry during positive and negative affect. Psychophysiology 16, 202–203.

Deckel, A.W., Lillaney, R., Ronan, P.J., Summers, C.H., 1998. Lateralized effects of ethanol on aggression and serotonergic systems in *Anolis carolinensis*. Brain Research 807, 38–46.

Ekman, P., Davidson, R.J., 1993. Voluntary smiling changes regional brain activity. Psychological Science 4, 342–345.

Ekman, P., Friesen, W.V., 1975. Unmasking the face: a guide to recognizing emotions from facial clues. Prentice-Hall, Englewood Cliffs, NJ.

Elgavish, E., Halpern, D., Dikman, Z., Allen, J.J.B., 2003. Does frontal EEG asymmetry moderate or mediate responses to the international affective picture system (IAPS)? Psychophysiology 40, S38.

Gable, P.A., Harmon-Jones, E., 2008. Relative left frontal activation to appetitive stimuli: considering the role of individual differences. Psychophysiology 45, 275–278.

Gable, P.A., Harmon-Jones, E., 2009. Postauricular reflex responses to pictures varying in valence and arousal. Psychophysiology 46, 487–490.

Gainotti, G., 1972. Emotional behavior and hemispheric side of the lesion. Cortex 8, 41–55.

Gasparrini, W.G., Satz, P., Heilman, K., Coolidge, F.L., 1978. Hemispheric asymmetries of affective processing as determined by the Minnesota Multiphasic Personality Inventory. Journal of Neurology, Neurosurgery and Psychiatry 41, 470–473.

Goldstein, K., 1939. The Organism: An Holistic Approach to Biology, Derived from Pathological Data in Man. American Book, New York.

Graham, R., Cabeza, R., 2001. Event-related potentials of recognizing happy and neutral faces. Neuroreport 12, 245–248.

Gray, J.A., 1994. Three fundamental emotion systems. In: Ekman, P., Davidson, R.J. (Eds.), The Nature of Emotion: Fundamental Questions. Oxford University Press, New York, pp. 243–247.

Gross, J.J., Levenson, R.W., 1993. Emotional suppression: physiology, self-report, and expressive behavior. Journal of Personality and Social Psychology 64, 970–986.

Güntürkün, O., Diekamp, B., Manns, M., Nottelmann, F., Prior, H., Schwarz, A., Skiba, M., 2000. Asymmetry pays: visual lateralization improves discrimination success in pigeons. Current Biology 10, 1079–1081.

Gur, R.C., Skolnick, B.E., Gur, R.E., 1994. Effects of emotional discrimination tasks on cerebral blood flow: Regional activation and its relation to performance. Brain and Cognition 25, 271–285.

Hagemann, D., 2004. Individual differences in anterior EEG asymmetry: methodological problems and solutions. Biological Psychology 67, 157–182.

Hagemann, D., Hewig, J., Seifert, J., Naumann, E., Bartussek, D., 2005. The latent state-trait structure of resting EEG asymmetry: replication and extension. Psychophysiology 42, 740–752.

Hagemann, D., Naumann, E., Becker, G., Maier, S., Bartussek, D., 1998. Frontal brain asymmetry and affective style: a conceptual replication. Psychophysiology 35, 372–388.

Hagemann, D., Naumann, E., Thayer, J.F., Bartussek, D., 2002. Does resting EEG asymmetry reflect a trait? An application of latent state-trait theory. Journal of Personality and Social Psychology 82, 619–641.

Harmon-Jones, E., 2003. Anger and the behavioural approach system. Personality and Individual Differences 35, 995–1005.

Harmon-Jones, E., Peterson, C.K., 2008. Effect of trait and state approach motivation on aggressive inclinations. Journal of Research in Personality 42, 1381–1385.

Harmon-Jones, E., 2004. On the relationship of anterior brain activity and anger: examining the role of attitude toward anger. Cognition and Emotion 18, 337–361.

Harmon-Jones, E., 2006. Unilateral right-hand contractions cause contralateral alpha power suppression and approach motivational affective experience. Psychophysiology 43, 598–603.

Harmon-Jones, E., 2007. Trait anger predicts relative left frontal cortical activation to anger-inducing stimuli. International Journal of Psychophysiology 66, 154–160.

Harmon-Jones, E., Abramson, L.Y., Sigelman, J., Bohlig, A., Hogan, M.E., Harmon-Jones, C., 2002. Proneness to hypomania/mania or depression and asymmetric frontal cortical responses to an anger-evoking event. Journal of Personality and Social Psychology 82, 610–618.

Harmon-Jones, E., Abramson, L.Y., Nusslock, R., Sigelman, J.D., Urosevic, S., Turonie, L.D., Alloy, L.B., Fearn, M., 2008a. Effect of bipolar disorder on left frontal cortical responses to goals differing in valence and task difficulty. Biological Psychiatry 63, 693–698.

Harmon-Jones, E., Allen, J.J.B., 1997. Behavioral activation sensitivity and resting frontal EEG asymmetry: covariation of putative indicators related to risk for mood disorders. Journal of Abnormal Psychology 106, 159–163.

Harmon-Jones, E., Allen, J.J.B., 1998. Anger and prefrontal brain activity: EEG asymmetry consistent with approach motivation despite negative affective valence. Journal of Personality and Social Psychology 74, 1310–1316.

Harmon-Jones, E., Gable, P.A., 2009. Neural activity underlying the effect of approach-motivated positive affect on narrowed attention. Psychological Science 20, 406–409.

Harmon-Jones, E., Harmon-Jones, C., Fearn, M., Sigelman, J.D., Johnson, P., 2008b. Action orientation, relative left frontal cortical activation, and spreading of alternatives: a test of the action-based model of dissonance. Journal of Personality and Social Psychology 94, 1–15.

Harmon-Jones, E., Lueck, L., Fearn, M., Harmon-Jones, C., 2006. The effect of personal relevance and approach-related action expectation on relative left frontal cortical activity. Psychological Science 17, 434–440.

Harmon-Jones, E., Peterson, C.K. Supine body position reduces neural response to anger evocation. Psychological Science, in press.

Harmon-Jones, E., Peterson, C.K., Harris, C.R., 2009. Jealousy: novel methods and neural correlates. Emotion 9, 113–117.

Harmon-Jones, E., Sigelman, J.D., 2001. State anger and prefrontal brain activity: evidence that insult-related relative left-prefrontal activation is associated with experienced anger and aggression. Journal of Personality and Social Psychology 80, 797–803.

Harmon-Jones, E., Sigelman, J.D., Bohlig, A., Harmon-Jones, C., 2003. Anger, coping, and frontal cortical activity: the effect of coping potential on anger-induced left frontal activity. Cognition and Emotion 17, 1–24.

Harmon-Jones, E., Vaughn-Scott, K., Mohr, S., Sigelman, J., Harmon-Jones, C., 2004. The effect of manipulated sympathy and anger on left and right frontal cortical activity. Emotion 4, 95–101.

Hellige, J.B., 1993. Hemispheric Asymmetry: What's Right and What's Left. Harvard University Press, Cambridge, MA.

Henriques, J.B., Davidson, R.J., 1990. Regional brain electrical asymmetries discriminate between previously depressed and healthy control subjects. Journal of Abnormal Psychology 99, 22–31.

Hewig, J., Hagemann, D., Seifert, J., Naumann, E., Bartussek, D., 2004. On the selective relation of frontal cortical activity and anger-out versus anger-control. Journal of Personality and Social Psychology 87, 926–939.

Hopkins, W.D., Bennett, A.J., Bales, S.L., Lee, J., Ward, J.P., 1993. Behavioral laterality in captive bonobos (*Pan paniscus*). Journal of Comparative Psychology 107, 403–410.

Izard, C.E., 1991. The Psychology of Emotions. Plenum Press, New York.

Jacobs, G.D., Snyder, D., 1996. Frontal brain asymmetry predicts affective style in men. Behavioral Neuroscience 110, 3–6.

Jensen-Campbell, L.A., Knack, J.M., Waldrip, A.M., Campbell, S.D., 2007. Do big five personality traits associated with self-control influence the regulation of anger and aggression? Journal of Research in Personality 41, 403–424.

Johnson, S.L., Ruggero, C.J., Carver, C.S., 2005. Cognitive, behavioral, and affective responses to reward: links with hypomanic symptoms. Journal of Social and Clinical Psychology 24, 894–906.

Johnson, S.L., Sandrow, D., Meyer, B., Winters, R., Miller, I., Solomon, D., Keitner, G., 2000. Increases in manic symptoms after life events involving goal attainment. Journal of Abnormal Psychology 109, 721–727.

Kalin, N.H., Larson, C., Shelton, S.E., Davidson, R.J., 1998. Asymmetric frontal brain activity, cortisol, and behavior associated with fearful temperament in rhesus monkeys. Behavioral Neuroscience 112, 286–292.

Kamiya, J., 1979. Autoregulation of the EEG alpha rhythm: a program for the study of consciousness. In: Peper, S.A.E., Quinn, M. (Eds.), Mind/Body Integration: Essential Readings in Biofeedback. Plenum Press, New York, pp. 289–297.

Kano, K., Nakamura, M., Matsuoka, T., Iida, H., Nakajima, T., 1992. The topographical features of EEGs in patients with affective disorders. Electroencephalography and Clinical Neurophysiology 83, 124–129.

Kayser, J., Bruder, G.E., Tenke, C.E., Stewart, J.W., Quitkin, F.M., 2000. Event-related potentials (ERPs) to hemifield presentations of emotional stimuli: Differences between depressed patients and healthy adults in P3 amplitude and asymmetry. International Journal of Psychophysiology 36, 211–236.

Kayser, J., Tenke, C., Nordby, H., Hammerborg, D., Hugdahl, K., Erdmann, G., 1997. Event-related potential (ERP) asymmetries to emotional stimuli in a visual half-field paradigm. Psychophysiology 34, 414–426.

Keil, A., Müller, M.A., Gruber, T., Wienbruch, C., Stolarova, M., Elbert, T., 2001. Effects of emotional arousal in the cerebral hemispheres: a study of oscillatory brain activity and event-related potentials. Clinical Neurophysiology 112, 2057–2068.

King, J.A., Rosal, M.C., Ma, Y., Reed, G., Kelly, T., Stanek III, E.J., Ockene, I.S., 2000. Sequence and seasonal effects of salivary cortisol. Behavioral Medicine 26, 67–73.

Knoch, D., Gianotti, L.R.R., Pascual-Leone, A., Treyer, V., Regard, M., Hohmann, M., Brugger, P., 2006. Disruption of right prefrontal cortex by low-frequency repetitive transcranial magnetic stimulation induces risk-taking behavior. The Journal of Neuroscience 26, 6469–6472.

Kolb, B., Taylor, L., 1991. Affective behavior in patients with localized cortical excisions: Role of lesion site and side. Science 214, 89–90.

Kotchoubey, B., Kubler, A., Strehl, U., Flor, H., Birbaumer, N., 2002. Can humans perceive their brain states? Consciousness and Cognition 11, 98–113.

Lagerspetz, K.M.J., 1969. Aggression and aggressiveness in laboratory mice. In: Garattini, S., Sigg, E.B. (Eds.), Aggressive Behavior. Wiley, New York, pp. 77–85.

Lang, P.J., 1995. The emotion probe. American Psychologist 50, 372–385.

Lang, P.J., Bradley, M.M., Cuthbert, B.N., 2008. International affective picture system (IAPS): Affective ratings of pictures and instruction manual. Technical Report A-8. University of Florida, Gainesville, FL.

Lewis, M., Alessandri, S.M., Sullivan, M.W., 1990. Violation of expectancy, loss of control, and anger expressions in young infants. Developmental Psychology 26, 745–751.

Lewis, M., Sullivan, M.W., Ramsey, D.S., Alessandri, S.M., 1992. Individual differences in anger and sad expressions during extinction: antecedents and consequences. Infant Behavior and Development 15, 443–452.

Meyer, B., Johnson, S.L., Carver, C.S., 1999. Exploring behavioral activation and inhibition sensitivities among college students at risk for bipolar spectrum symptomatology. Journal of Psychopathology and Behavioral Assessment 21, 275–292.

Meyer, B., Johnson, S.L., Winters, R., 2001. Responsiveness to threat and incentive in bipolar disorder: relations of the BIS/BAS scales with symptoms. Journal of Psychopathology and Behavioral Assessment 23, 133–143.

Miller, P.A., Eisenberg, N., 1988. The relation of empathy to aggressive and externalizing/antisocial behavior. Psychological Bulletin 103, 324–344.

Murphy, F.C., Nimmo-Smith, I., Lawrence, A.D., 2003. Functional neuroanatomy of emotion: a meta-analysis. Cognitive, Affective, & Behavioral Neuroscience 3, 207–233.

Nayyar, K., Cochrane, R., 1996. Seasonal changes in affective state measured prospectively and retrospectively. British Journal of Psychiatry 168, 627–632.

Nusslock, R., Abramson, L.Y., Harmon-Jones, E., Alloy, L.B., Hogan, M.E., 2007. A goal-striving life event and the onset of hypomanic and depressive episodes and symptoms: Perspective from the behavioral approach system (BAS) dysregulation theory. Journal of Abnormal Psychology 116, 105–115.

Ohgami, Y., Kotani, Y., Tsukamoto, T., Omura, K., Inoue, Y., Aihara, Y., Nakayama, M., 2006. Effects of monetary reward and punishment on stimulus-preceding negativity. Psychophysiology 43, 227–236.

Oyane, N.M.F., Bjelland, I., Pallesen, S., Holsten, F., Bjorvatn, B., 2008. Seasonality is associated with anxiety and depression: the Hordaland health study. Journal of Affective Disorders 105, 147–155.

Partonen, T., Lonnqvist, J., 1998. Seasonal affective disorder. Lancet 352, 1369–1374.

Perria, P., Rosadini, G., Rossi, G.F., 1961. Determination of side of cerebral dominance with Amobarbital. Archives of Neurology 4, 175–181.

Peterson, C.K., Gable, P., Harmon-Jones, E., 2008a. Asymmetric frontal ERPs, emotion, and behavioral approach/inhibition sensitivity. Social Neuroscience 3, 113–124.

Peterson, C.K., Harmon-Jones, E., 2009. Circadian and seasonal variability of resting frontal EEG asymmetry. Biological Psychology 80, 315–320.

Peterson, C.K., Shackman, A.J., Harmon-Jones, E., 2008b. The role of asymmetric frontal cortical activity in aggression. Psychophysiology 45, 86–92.

Pizzagalli, D., Shackman, A.J., Davidson, R.J., 2003. The functional neuroimaging of human emotion: asymmetric contributions of cortical and subcortical circuitry. In: Hugdahl, K., Davidson, R.J. (Eds.), The Asymmetric Brain. MIT Press, Cambridge, MA, pp. 511–532.

Pizzagalli, D.A., Sherwood, R.J., Henriques, J.B., Davidson, R.J., 2005. Frontal brain asymmetry and reward responsiveness: a source-localization study. Psychological Science 16, 805–813.

Plant, E.A., Devine, P.G., 1998. Internal and external motivation to respond without prejudice. Journal of Personality and Social Psychology 75, 811–832.

Plant, E.A., Devine, P.G., 2001. Responses to other-imposed pro-Black pressure: acceptance or backlash. Journal of Experimental Social Psychology 37, 486–501.

Plant, E.A., Devine, P.G., 2003. The antecedents and implications of interracial anxiety. Personality and Social Psychology Bulletin 29, 790–801.

Plutchik, R., 1980. Emotion: A Psychoevolutionary Synthesis. Harpercollins College Division, New York, NY.

Putman, P., Hermans, E., van Honk, J., 2004. Emotional Stroop performance for masked angry faces: It's BAS, not BIS. Emotion 4, 305–311.

Reid, S.A., Duke, L.M., Allen, J.J.B., 1998. Resting frontal electroencephalographic asymmetry in depression: inconsistencies suggest the need to identify mediating factors. Psychophysiology 35, 389–404.

Rilling, J.K., Winslow, J.T., O'Brien, D., Gutman, D.A., Hoffman, J.M., Kilts, C.D., 2001. Neural correlates of maternal separation in rhesus monkeys. Biological Psychiatry 49, 146–157.

Rinn, W.E., 1984. The neuropsychology of facial expression: a review of the neurological and psychological mechanisms for producing facial expressions. Psychological Bulletin 95, 52–77.

Riskind, J.H., Gotay, C.C., 1982. Physical posture: Could it have regulatory or feedback effects on motivation and emotion? Motivation and Emotion 6, 273–298.

Robinson, R.G., Price, T.R., 1982. Post-stroke depressive disorders: a follow-up study of 103 patients. Stroke 13, 635–641.

Rogers, L.J., 2002. Lateralised brain function in anurans: comparison to lateralisation in other vertebrates. Laterality: Asymmetries of Body, Brain and Cognition 7, 219–239.

Rossi, G.F., Rosadini, G.R., 1967. Experimental analyses of cerebral dominance in man. In: Millikan, D.H., Darley, F.L. (Eds.), Brain Mechanisms Underlying Speech and Language. Grune & Stratton, New York.

Sackeim, H., Greenberg, M.S., Weimen, A.L., Gur, R.C., Hungerbuhler, J.P., Geschwind, N., 1982. Hemispheric asymmetry in the expression of positive and negative emotions: neurologic evidence. Archives of Neurology 39, 210–218.

Schaffer, C.E., Davidson, R.J., Saron, C., 1983. Frontal and parietal electroencephalogram asymmetry in depressed and nondepressed subjects. Biological Psychiatry 18, 753–762.

Schiff, B.B., Lamon, M., 1989. Inducing emotion by unilateral contraction of facial muscles: a new look at hemispheric specialization and the experience of emotion. Neuropsychologia 27, 923–935.

Schiff, B.B., Lamon, M., 1994. Inducing emotion by unilateral contraction of hand muscles. Cortex 30, 247–254.

Schmidt, L.A., Fox, N.A., Rubin, K.H., Sternberg, E.M., Gold, P.W., Smith, C.C., Schulkin, J., 1997. Behavioral and neuroendocrine responses in shy children. Developmental Psychobiology 30, 127–140.

Schulkin, J., Gold, P.W., McEwen, B.S., 1998. Induction of corticotropin-releasing hormone gene expression by gluco-corticoids: implication for understanding the states of fear and anxiety and allostatic load. Psychoneuroendocrinology 23, 219–243.

Schutter, D.J.L.G., 2009. Transcranial magnetic stimulation. In: Harmon-Jones, E., Beer, J.S. (Eds.), Methods in Social Neuroscience. Guilford, New York, pp. 233–258.

Schutter, D.J.L.G., van Honk, J., d'Alfonso, A.A.L., Postma, A., de Haan, E.H.F., 2001. Effects of slow rTMS at the right dorsolateral prefrontal cortex on EEG asymmetry and mood. Neuroreport 12, 445–447.

Siniatchkin, M., Kropp, P., Gerber, W.-D., 2000. Neurofeedback—the significance of reinforcement and the search for an appropriate strategy for the success of self-regulation. Applied Psychophysiology and Biofeedback 25, 167–175.

Smits, D.J.M., Kuppens, P., 2005. The relations between anger, coping with anger, and aggression, and the BIS/BAS system. Personality and Individual Differences 39, 783–793.

Spielberger, C.D., 1988. State–Trait Anger Expression Inventory. Psychological Assessment Resources, Orlando, FL.

Spielberger, C.D., Reheiser, E.C., Sydeman, S.J., 1995. Measuring the experience, expression, and control of anger. In: Kassinove, H. (Ed.), Anger Disorders: Definition, Diagnosis, and Treatment. Series in Clinical and Community Psychology, Taylor & Francis, Philadelphia, pp. 49–67.

Sutton, S.K., Davidson, R.J., 1997. Prefrontal brain asymmetry: a biological substrate of the behavioral approach and inhibition systems. Psychological Science 8, 204–210.

Terzian, H., Cecotto, C., 1959. Determination and study of hemisphere dominance by means of intracarotid sodium amytal injection in man: II. Electroencephalographic effects. Bolletino della Societa Ztaliana Sperimentale 35, 1626–1630.

Thomas, S.J., Johnstone, S.J., Gonsalvez, C.J., 2007. Event-related potentials during an emotional Stroop task. International Journal of Psychophysiology 63, 221–231.

Tomarken, A.J., Davidson, R.J., Henriques, J.B., 1990. Resting frontal brain asymmetry predicts affective responses to films. Journal of Personality and Social Psychology 59, 791–801.

Tomarken, A.J., Davidson, R.J., Wheeler, R.E., Doss, R., 1992. Individual differences in anterior brain asymmetry and fundamental dimensions of emotion. Journal of Personality and Social Psychology 62, 676–687.

Tops, M., Wijers, A.A., van Staveren, A.S., Bruin, K.J., Den Boer, J.A., Meijman, T.F., Korf, J., 2005. Acute cortisol administration modulates EEG alpha asymmetry in volunteers. Biological Psychology 69, 181–193.

Van Cauter, E., 1989. Physiology and pathology of circadian rhythms. In: Edwards, C.R.W., Lincoln, D.W. (Eds.), Recent Advances in Endocrinology and Metabolism. Churchill Livingstone, Edinburgh, UK, pp. 109–134.

van de Laar, M.C., Licht, R., Franken, I.H.A., Hendriks, V.M., 2004. Event-related potentials indicate motivational relevance of cocaine cues in abstinent cocaine addicts. Psychopharmacology 177, 121–129.

van Honk, J., Schutter, D.J.L.G., 2006. From affective valence to motivational direction: the frontal asymmetry of emotion revisited. Psychological Science 17, 963–965.

van Honk, J., Tuiten, A., de Haan, E., van den Hout, M., Stam, H., 2001. Attentional biases for angry faces: relationships to trait anger and anxiety. Cognition and Emotion 15, 279–297.

van Honk, J., Tuiten, A., van den Hout, M., Koppeschaar, H., Thijssen, J., de Haan, E., Verbaten, R., 1998. Baseline salivary cortisol levels and preconscious selective attention for threat: a pilot study. Psychoneuroendocrinology 23, 741–747.

van Honk, J., Tuiten, A., Verbaten, R., van den Hout, M., Koppeschaar, H., Thijssen, J., de Haan, E., 1999. Correlations among salivary testosterone, mood, and selective attention to threat in humans. Hormones and Behavior 36, 17–24.

Verona, E., Sadeh, N., Curtin, J.J., 2009. Stress-induced asymmetric frontal brain activity and aggression risk. Journal of Abnormal Psychology 118, 131–145.

Wacker, J., Heldmann, M., Stemmler, G., 2003. Separating emotion and motivational direction in fear and anger: Effects on frontal asymmetry. Emotion 3, 167–193.

Wager, T.D., Phan, K.L., Liberzon, I., Taylor, S.F., 2003. Valence, gender, and lateralization of functional brain anatomy in emotion: a meta-analysis of findings from neuroimaging. Neuroimage 19, 513–531.

Walker, B.R., Best, R., Noon, J.P., Watt, G.C., Webb, D.J., 1997. Seasonal variation in glucocorticoid activity in healthy men. Journal of Clinical Endocrinology and Metabolism 82, 4015–4019.

Watson, D., 2000. Mood and Temperament. Guilford Press, New York.

Watson, D., Wiese, D., Vaidya, J., Tellegen, A., 1999. The two general activation systems of affect: structural findings, evolutionary considerations, and psychobiological evidence. Journal of Personality and Social Psychology 76, 820–838.

Wheeler, R.E., Davidson, R.J., Tomarken, A.J., 1993. Frontal brain asymmetry and emotional reactivity: a biological substrate of affective style. Psychophysiology 30, 82–89.

Wilson, F.A., O'Scalaidhe, S.P., Goldman-Rakic, P.S., 1994. Functional synergism between putative gamma-aminobutyrate containing neurons and pyramidal neurons in prefrontal cortex. Proceedings National Academy of Sciences of United States of America 26, 4009–4013.

Wirz-Justice, A., 2005. Chronobiological strategies for unmet needs in the treatment of depression. Medicographia 27, 223–227.

Wright, R.A., Tunstall, A.M., Williams, B.J., Goodwin, J.S., Harmon-Jones, E., 1995. Social evaluation and cardiovascular response: an active coping approach. Journal of Personality and Social Psychology 69, 530–543.

Young, P.T., 1943. Emotion in Man and Animal: Its Nature and Relation to Attitude and Motive. John Wiley and Sons, New York.

Zinner, L.R., Brodish, A.B., Devine, P.G., Harmon-Jones, E., 2008. Anger and asymmetric frontal cortical activity: evidence for an anger-withdrawal relationship. Cognition & Emotion 22, 1081–1093.