The frontal laterality of emotion: a historical overview

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The processing and experience of emotions in humans are complex phenomena that involve a brain circuitry of cortical and subcortical structures. Amongst the most successful cortical centred theories in affective and social neuroscience is the frontal asymmetry of emotion model. Early views on emotion in humans predominantly implicated the right hemisphere in the processing of emotions. In the late 1970s, evidence was provided that positive and negative affect was associated with patterns of left and right frontal brain activity, respectively. Building on motives of approach- and avoidance-related emotions, more recent electrophysiological studies have found support for left hemispheric involvement in the processing of the approach-related emotion anger. Finally, transcranial magnetic stimulation studies have added causal evidence for the lateralised involvement of the left prefrontal cortex in the approach-related emotion anger and the right prefrontal cortex in the avoidance-related emotion fear. Current research focuses on the role of functional connectivity between the hemispheres to further elucidate the neural underpinnings of emotion and emotional behaviour. (*Netherlands Journal of Psychology*, 64, 112-118.)

Keywords: Brain asymmetry; emotion; laterality; prefrontal cortex

One of the most successful cortical centred theories in affective and social neuroscience is the frontal asymmetry of emotion model. In 1978, Richard Davidson presented a paper describing relationships between the experience of emotions and differential patterns of asymmetrical frontal brain activity (Allen & Kline, 2004). Davidson demonstrated that the left prefrontal cortex (PFC) was involved in the processing of positive emotions, whereas the right PFC was involved in the processing of negative emotions. Interestingly, his proposal was against the prevailing theory that the right hemisphere was involved in emotional processing exclusively (Luys, 1881). The abstract of his presentation was among the first publications describing the use of the electroencephalogram (EEG) in cortical laterality research on emotions (Davidson, Schwartz, Saron, Bennett, & Goleman, 1979). Particularly in the last ten years, Davidson's frontal lateralisation model has been extensively investigated and new insights have contributed to the

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development of alternative frontal lateralisation models of emotions. The aim of this paper is to provide a brief historical overview of the cortical lateralisation theories of emotion.

The emotional brain

Emotions are complex phenomena which are closely related to motivation and action readiness (Frijda, 1986). Ross Buck (1999) defined motivation as: 'the potential for behaviour that is built into a system of behaviour control (p.303)', and emotion as 'the readout of motivational potential when activated by a challenging stimulus (p.303)'.

On the neuronal level the processing and experience of emotions involves a complex circuitry comprised of cortical and subcortical structures (James, 1884: Papez, 1937: Damasio, 1994: LeDoux, 1996). Even though researchers generally agree upon the brain structures involved in motivation and emotion, theories differ in their emphasis on either subcortical or cortical structures. For instance, in LeDoux' model of emotive processing, two pathways are distinguished. The first pathway involves a fast thalamo-amygdaloid route, and enables rapid reflex-like actions in terms of fight-flight behaviour. The second pathway, a relatively slower thalamo-cortical route operating in parallel with the fast thalamo-amygdaloid route involves the visual cortex, and allows a more elaborate cognitive evaluation of the affective stimulus (LeDoux, 1996). According to the somatic-marker hypothesis, a central role is reserved for the ventromedial PFC (vmPFC) (Damasio, 1994). In the somatic-marker hypothesis, which is in fact similar to the ideas of William James (1884), Damasio proposes that emotions arise from bodily responses generated by the autonomous nervous system in response to biologically relevant events. Somatic markers are initiated by the amygdala and evaluated in the vmPFC allowing humans to consciously work their way through situations of complexity and ambiguity (Dalgeish, 2004). These assumptions are supported by lesion studies showing that individuals with vmPFC and amygdala damage show disadvantageous risky decision-making. (Bechara, Damasio, Damasio, & Lee, 1999). It is suggested that vmPFC lesions result in the inability to evaluate somatic markers, whereas amygdala lesions result in the absence of somatic markers to guide decision-making appropriately. In figure 1, brain regions involved in emotion and motivation are highlighted.

Even though the PFC is generally assumed to play a role in emotion processing, studies into the exact nature of PFC involvement in emotions have given rise to one of the most successful cortical centred theories in affective and social neuroscience: The frontal asymmetry of emotion model.

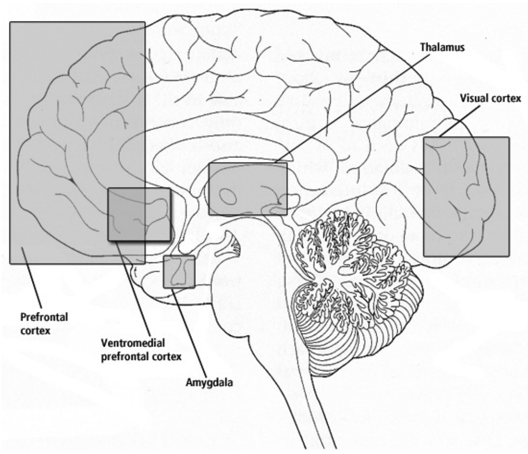

Figure 1
Brain regions involved in motivation and emotion.

Frontal laterality and affective valence

The notion of asymmetrical hemispheric engagement in emotional processing was formulated as early as the late 19th century (Luys, 1881). Almost 100 years later, in the mid 1970s, Schwartz, Davidson, and Maer (1975) published a paper in which the right hemisphere of the healthy human brain is implicated in general emotional processing. The authors demonstrated increased right hemispheric activation when confronting subjects with emotional questions as compared with non-emotional questions. Lateral eye movements were used to measure hemispheric engagement (Schwartz et al. 1975). Using this method, Schwartz and colleagues showed that increased right hemispheric activation was linked to emotional and spatial processing, whereas increased left hemispheric activity was associated with non-emotional and verbal processing. During the 1978 annual meeting of the Society for Psychophysiological Research, Davidson presented a paper suggesting that experiences of positive and negative effect are reflected by differential patterns of asymmetrical frontal activity (for a review see Allen & Kline, 2004). The abstract of this presentation was published in 1979 in *Psychophysiology* as the first publication using electroencephalographic (EEG) recordings in the study on the frontal lateralisation of emotion (Davidson, Schwartz, Saron, Bennett, & Goleman, 1979). In this paper, Davidson and colleagues proposed a lateralisation of positive emotions to the left PFC and negative emotions to the right PFC. This distinction between positive and negative affect being lateralised to the left and right, respectively, has become known as the *Valence Model*. Evidence supporting the lateralised involvement of the left and right PFC in positive and negative emotions was provided by an electrophysiological study, showing that positive-emotion eliciting questions yielded increases in left PFC activity, whereas negative-emotion eliciting questions showed decreases in right PFC activity (Ahern & Swartz, 1985). In further support of the valence model, it was demonstrated that EEG asymmetries predicted the difference between experienced positive and negative affect (Tomarken, Davidson, & Henriques, 1990). Positively rated video clips were associated with increased relative left activity, whereas negatively rated video clips were associated with increased relative right-sided activity. In addition to state-related changes on PFC activity, it was also shown that the relation between resting state EEG asymmetries and positive and negative affect is stable over time. (Tomarken, Davidson, Wheeler, & Doss, 1992). This suggests that frontal EEG asymmetries may reflect stable trait-like personality characteristics in terms of the propensity to experience positive or negative affect.

In one of the first reviews, a plethora of experimental results supporting the positive-negative distinction in the cerebral hemispheres was discussed and three possible variants of emotion lateralisation were considered: (1) Emotions are better recognised by the right hemisphere, (2) Control of emotional expression generally takes place in the right hemisphere, and (3) The right hemisphere is specialised for dealing with negative emotions and the left hemisphere is specialised for dealing with positive emotions. (Silberman & Weingarter, 1986). As noted by the authors, many of the results needed replication and the mechanisms underlying frontal lateralisation were still not well understood. Nonetheless, it was concluded that the available evidence provided support for the view that emotions are processed by the PFC in lateralised fashion.

In sum, state and trait positive affect is associated with increased relative left frontal activity, whereas state and trait negative affect is associated with increased relative right frontal activity.

However, the vast majority of the research on the *Valence Model* was conducted using the Positive and Negative Affect Scale (PANAS) (Watson, Clark, & Tellegen, 1988). Affects that are assessed by the PANAS include attentiveness, interestedness, alertness, enthusiasm, excitement and inspiration for positive affects, and distress, hostility, irritability, anxiety and shame for the negative affects (Crawford & Henry, 2004). Since the positive affect scale includes words such as ‘interested’, and the negative scale includes words such as ‘afraid’, several theorists argued that the self-report that results from the scale might be confounded with approach- and withdrawal-related motivation (Watson, Wiese, Vaidya, & Tellegen, 1999).

From affective valence to motivational direction

The lateralised involvement of the PFC in the processing of positive and negative emotions has yielded a substantial body of evidence in support of the valence model. However, in the late 1990s, research started to appear in the literature that yielded conflicting results (Harmon-Jones, 2003). In this research, the underlying assumption that approach-related motivation is associated with positive emotions was questioned. Harmon-Jones and Allen (1997) introduced the concept of approach and withdrawal-related motivation in the PFC lateralisation theory of emotion. In one of their first experiments, Harmon-Jones and Allen (1997) determined participants’ baseline EEG asymmetry to measure relative hemispheric dominance. The motivational tendency to approach was measured by the behavioural activation scales (BAS), whereas the motivational tendency to withdrawal was measured by the behavioural inhibition scales (BIS) (Carver & White, 1994, Gray, 1981). Results showed that the BAS score was related to a dominant left-sided PFC asymmetry. Trait BIS, however, yielded no significant relation with relative right PCF activity, arguably because of the discrepancy between the conceptualisations of the withdrawal system as postulated by Davidson and the BIS in terms of avoidance as originally defined by Gray (Harmon-Jones & Allen, 1997).

Anger and motivational direction

The introduction of approach- and withdrawal-related emotions in the PFC model of emotions has resulted in an alternative model that has discarded the valence component. In the motivational direction model, approach-related emotions are lateralised to the left PFC, whereas avoidance-related emotions are lateralised to the right PFC. In this model, the negative emotion anger is associated with approach-related behaviour and lateralised to the left PFC (Harmon-Jones & Allen, 1998). In this model it is assumed that anger is associated with approach-related tendencies and can result in, for instance, aggressive behaviour. In additional research evaluating the motivational direction and affective valence model two alternative relationships between trait anger and frontal cortical activity were hypothesised: 1) If the asymmetry in frontal cortical activity represents emotional valence, then higher trait anger should be reflected in relatively higher right hemispheric frontal activity; 2) If the asymmetry in frontal cortical activity represents motivational direction, then higher trait anger should be reflected in relatively higher left hemispheric frontal activity (Harmon-Jones & Allen, 1998).

Results showed that trait anger as measured by the Buss and Perry Aggression Questionnaire

(Buss & Perry, 1992) was correlated to relatively greater left frontal activity.

In another study by Harmon-Jones (2004a) it was shown that a positive attitude toward anger did not correlate with the relative left over right frontal activity. These results demonstrate that even relatively positive attitudes toward anger could not account for the reported relation between trait anger and relative left over right frontal activity.

Furthermore, the relationship between relative left over right prefrontal activity and state-induced anger was further explored in an experiment where volunteers were deliberately insulted (Harmon-Jones & Sigelman, 2001). In accordance with their hypothesis it was shown that insulted participants demonstrated a significant increase in left PFC activity and were more likely to act aggressively.

In sum, this research strengthens the claim that, despite its negative valence, the processing of the emotion anger is lateralised to the left PFC.

Intensity of approach-related motivational tendencies

Based on the previous research it can be assumed that anger is associated with approach-related motivational tendencies. Motivational theories have stressed the importance of motivational intensity and claim that motivational intensity is determined by the expectancy of success and task difficulty (Brehm & Self, 1989). Furthermore, approach-related motivation is associated with a dominant pattern of relative left prefrontal activity. Taking this latter notion into account, it can therefore be expected that, if no approach-related tendencies can be exercised, the relative left frontal activity will be less pronounced. The intensity of motivation can be manipulated and changes in frontal asymmetrical activity can be recorded in order to examine this possibility (Harmon-Jones, Lueck, Fearn, & Harmon-Jones, 2006). Results showed that in action-possible conditions, participants showed a larger left-to-right increase in PFC activity as compared with participants in action-impossible conditions (Harmon-Jones, et al., 2006). In sum, these findings suggest that motivation intensity is positively associated with left PFC activity and approach-related behaviour.

Thus far, research demonstrating that approach-related tendencies are lateralised to the left and withdrawal-related tendencies are lateralised to the right prefrontal cortex has mainly been correlational by nature. These correlational findings show that brain activity and function are statistically related. However, it does not tell us whether this frontal brain asymmetry is causally related to the differences in approach and withdrawal-related behaviours.

In the cognitive and affective neurosciences, one of the few instruments able to demonstrate causal relationships between brain and behaviour is transcranial magnetic stimulation (TMS) (Schutter, van Honk, & Panksepp, 2004). TMS is a safe, non-invasive technique which is based on Faraday's law of electromagnetic induction, and uses magnetic fields to modulate cortical brain activity (for reviews see Bohning, 2000; Schutter & van Honk, 2002). When TMS is applied repetitively (rTMS) with frequencies around 1 Hz cortical excitability is reduced, whereas stimulation frequencies of 5 Hz and greater increase cortical excitability (Wassermann, 1998).

The first slow frequency rTMS study addressing the issue of PFC asymmetry in the processing of anger deployed a pictorial emotional Stroop task (d'Alfonso, van Honk, Hermans, Postma, & de Haan, 2000). The pictorial emotional Stroop task is a modified version of the colour-naming Stroop task. In the pictorial emotional Stroop task, subjects are instructed to name the colour of facial expressions as fast as possible. The mean colour-naming latencies of emotional facial expressions minus the colour-naming latencies of neutral facial expressions result in interference scores, an index of the processing of the emotional content of the facial expression presented. It was hypothesised that interference scores would increase following right PFC rTMS and would decrease following left PFC rTMS. In line with the hypotheses, right rTMS PFC resulted in selective attention to angry facial expressions, whereas left PFC rTMS resulted in selective attention away from the angry facial expressions. These were the first results showing a direct association between the modulation of PFC and the processing of angry facial expressions in terms of approach- (i.e., interference scores) and withdrawal-related behaviour (i.e., facilitation scores). Additionally, this study introduced the concept of hemispheric balance into the motivational direction model.

Using fearful facial expressions, the motivational-direction asymmetry of emotion found further support by a sham-controlled low frequency rTMS to the right PFC (van Honk, Schutter, d'Alfonso, Kessels & de Haan, 2002). It was hypothesised that reduction in right cortical activity would result in a motivational shift towards approach-related behaviour, causing reduced attention to fearful facial expressions. Results showed vigilant attention for fearful facial expressions in response to the sham rTMS. Importantly, rTMS significantly reduced attention for fearful facial expressions demonstrating the hypothesised motivational shift towards approach-related behaviour. The shift in hemispheric dominance was demonstrated in an interleaved rTMS-EEG experiment which showed contralateral increases in brain activity following low frequency rTMS to the right PFC (Schutter, van Honk, d'Alfonso, Postma, & de Haan, 2001).

To provide further support for the motivational-direction model, anger but not happiness should be processed by the left frontal cortex. In a recent experiment, sham and active low frequency rTMS was applied over the left and right PFC and emotional memory for angry and happy facial expression was examined (van Honk & Schutter, 2006). The emotional memory task consisted of the presentation of a set of happy and neutral faces and a set of angry and neutral faces. After a 30-second presentation time the sets disappeared, and the faces reappeared in a random order on the top of the screen. Participants were instructed to place back the faces into their original position. In agreement with the motivational direction model, significant reductions in memory for angry faces was observed following left PFC rTMS as compared with both sham and right PFC rTMS. The processing of happy faces was not influenced by rTMS over the left PFC or the right PFC.

In sum, these results support the notion of a motivational-direction model of emotion processing. Figure 2 shows the displays used in the memory task (a) and results (b).

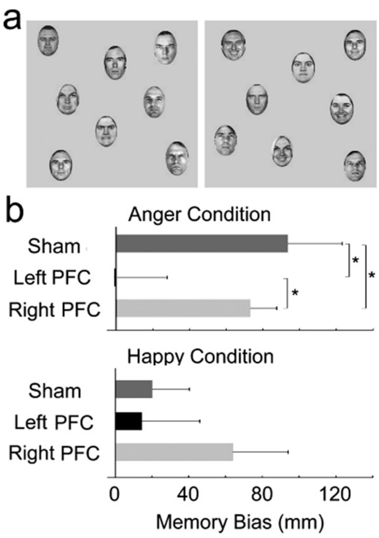

Figure 2
Displays used in the memory task and results. On each trial, a display of angry and neutral faces or a display of happy and neutral faces was presented for 30 s. The graphs show memory bias after repetitive transcranial magnetic stimulation (rTMS) of left prefrontal cortex (PFC) and right PFC and after sham rTMS. Asterisks indicate significant differences between conditions. Adapted from Van Honk and Schutter (2006) From affective valence to motivational direction: the frontal asymmetry of emotion revised. *Psychological Science, 17*, p 964.

Summary and discussion

There is ample evidence that the frontal cortex plays a central role in the conscious processing of emotionally laden stimuli. In the social and affective neurosciences, one the most successful cortical theories of emotion is the model of frontal asymmetry of emotion. Two core motivational action tendencies are suggested to be represented in the frontal hemispheres in a lateralised fashion, arguably to preclude conflict among action tendencies (Davidson, 1998, Harmon-Jones, 2003, van Honk & Schutter, 2006). Early pioneering work by Davidson and colleagues (1990) provided evidence for involvement of the left frontal hemisphere in approach-related positive emotions, whereas the right frontal hemisphere is concerned with withdrawal-related negative emotions. However, Harmon-Jones found conflicting results by showing that negative emotion anger is processed by the left hemisphere and proposed to remove the distinction between positive and negative emotions from the affective valence model (Harmon-Jones, 2004b). In support of Harmon-Jones' proposal, van Honk and Schutter (2006) recently demonstrated that low-frequency rTMS over the left PFC modulates the processing of angry, but not happy facial expressions. Figure 3 provides a historical perspective on the frontal asymmetry of emotion model.

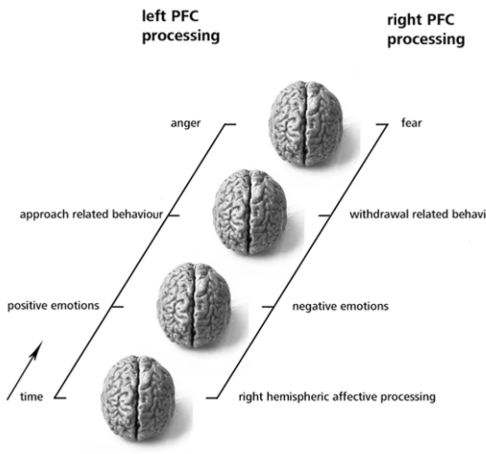

Figure 3
The frontal asymmetry model of emotion in historical perspective.

It should, however, be noted that the vast majority of the studies used EEG recordings to examine frontal asymmetries in emotion processing. Even though EEG is a valuable tool to measure electric brain activity from the scalp, the technique is correctional by nature and can only make course estimations on the actual neural sources of activity. As discussed above, rTMS can, however, provide direct insights into the brain-function relationship by modulating pre-specified cortical regions. By combining EEG and TMS, thereby creating the possibility to investigate the asymmetrical frontal activity from a more dynamic approach, the relationship between PFC activity and behavioural motivation can be further elucidated. For example, current research is now applying this kind of strategies to examine functional connectivity and information transfer between the cerebral hemispheres.

Finally, it should also be noted that the motivational-direction model is still under construction. Emotions that have been assessed in experimental paradigms include anger, fear and joy: emotions with a positive or negative valence provoking either approach- or withdrawal-related behaviour. For example, the withdrawal-related emotion disgust has not yet been addressed in research on the frontal asymmetry of emotion. Based on the motivational-direction model it can therefore be expected that the negative emotion disgust will be related to relative right frontal activity.

In conclusion, there is now abundant evidence that the left frontal cortex is predominantly involved in the approach-related negative emotion anger, whereas the right frontal cortex is mainly involved in the withdrawal-related negative emotion fear. In spite of the conceptual and methodological issues, the model provides a heuristic framework in which emotional processing can be studied.

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