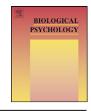
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Frontal brain asymmetry and transient cardiovascular responses to the perception of humor

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ABSTRACT

The study examined the relationship of individual differences in prefrontal brain asymmetry, measured by the EEG in resting conditions, to the individual's responsivity in the context of humor (n = 42). Several weeks after the EEG recording, immediate cardiovascular responses to the perception of humor and behavioral indicators of humor processing were obtained in an experimental paradigm involving non-verbal cartoons. Relatively greater resting activity in the left than right prefrontal cortex, particularly at the ventrolateral positions, was associated with faster detection of humor, a more pronounced cardiac response to the perception of humor (heart rate and cardiac output), and more accessible internal positive affective states (indicated by faster reports of amusement levels). The study confirms and extends findings of the relevance of prefrontal brain asymmetry to affective responsivity, contributing evidence in the domain of positive affect and humor, and demonstrating relationships to the immediate cardiovascular response pattern to an emotional event.

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1. Introduction

Well-established neuroscientific laterality models of affect and psychopathology assume the left and right prefrontal cortical hemispheres to be differentially involved in processes modulating affective responses to emotional challenges, thereby characterizing an individual's "affective style" (Davidson, 1998; for a review, see Harmon-Jones et al., 2010). Specifically, relative inactivity of left prefrontal regions, measured in resting conditions, is assumed to be related to an affective style associated with depression proneness (e.g., Nusslock et al., 2011; Pössel et al., 2008). It has also been suggested that a relatively lower left than right prefrontal resting activity may be associated with a less resilient response profile to emotional challenges (Koslov et al., 2011). Accordingly, findings indicated that individuals showing relative inactivity of left prefrontal regions at rest may be emotionally rigid and unresponsive to emotional events (Papousek et al., 2012).

A common method in the field to assess an individual's relative strength or weakness of left prefrontal functions is to measure the

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asymmetry pattern in the prefrontal cortex in resting conditions, typically by using the electroencephalogram (EEG). Evidence suggested that in this general context, the relative difference between the hemispheres is more important than the absolute level of independent left or right hemisphere activity per se. That is, no effect of increased left-hemisphere activity may be expected if the right hemisphere is more active, too (Davidson et al., 1990; Gur et al., 1994; Harmon-Jones, 2006; Heller et al., 1997). Consequently, relationships to other variables often have not been observed if only absolute activity at individual sites were examined and data of the left and the right hemisphere were not related to each other, for example, by the use of appropriate laterality coefficients (e.g., Blackhart and Kline, 2005; Cole et al., 2012; Harmon-Jones, 2006; Papousek and Schulter, 2004; Papousek et al., 2009; Shankman et al., 2011).

Although there is a great amount of literature on the laterality models of affect using EEG methods (for a review, see Harmon-Jones et al., 2010), to date relatively few studies in the field have been specifically concerned with specific response profiles. A recent study demonstrated that relatively greater left than right hemisphere (Left > Right) activity at rest, predominantly in the ventral lateral region of the prefrontal cortex, was associated with distinct and differentiated responses to the (positive and negative) mood induction. By contrast, participants with a Right > Left asymmetry pattern at rest appeared unresponsive to the stimulation (Papousek

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et al., 2012). Similarly, in a study of Coan and Allen (2003), a Left > Right prefrontal EEG asymmetry at rest predicted more intense (positive and negative) feelings during posed emotional facial expressions, observed for the ventrolateral and dorsolateral prefrontal electrodes. Furthermore, Koslov et al. (2011) reported an association between a Left > Right EEG asymmetry in the dorsolateral prefrontal cortex and a greater cardiac output response to a social stressor representing a more adaptive, approach-related response profile. These findings are in line with the idea that a Left > Right asymmetry pattern in the lateral prefrontal cortex is associated with greater emotional responsivity as compared to an asymmetry in favor of the right hemisphere (Papousek et al., 2012). Earlier studies found greater responses in Left > Right individuals to positive or approach-related stimulation in particular (Tomarken et al., 1990; Wheeler et al., 1993).

In depressed and anxious patients, attenuated emotional responsivity has been observed in response to negatively as well as positively valenced stimuli (Bylsma et al., 2008; Palm et al., 2011). But positive and negative responsivity may have different functional significance. For instance, Rottenberg et al. (2002) showed that lower responsivity to negative stimuli was predominantly related to concurrent impairment, whereas lower responsivity to positive (amusing) stimuli specifically predicted poor recovery from depression. Importantly, blunted responses in psychopathology have not only been shown for subjective but also for physiological responses to emotional challenges (Bylsma et al., 2008; Chida and Hamer, 2008; Hoehn-Saric and McLeod, 2000). Theoretical concepts such as "physiological flexibility" or "autonomic flexibility" focus on the importance of the ability to mount psychophysiological responses to environmental stimuli that support adaptive adjustments to changing demands (Dienstbier, 1989; Friedman and Thayer, 1998; Hoehn-Saric and McLeod, 2000; McEwen, 1998). In the above-mentioned study of Rottenberg et al. (2002), low heart rate reactivity to an amusing stimulus was even the strongest predictor of nonrecovery from depression, compared to a behavioral measure and responses to negative stimuli. Thus, transient cardiovascular responses to the perception of humor may indicate a relevant disposition in the context of mental health.

Two processes are happening in the immediate context of the perception of humor: the cognitive process of insight (of having "gotten the point") and the affective experience following it. According to humor theory, in order to perceive humor it is necessary to detect a conflict between two initially incongruent ideas, concepts, or situations that are brought together in a surprising or unexpected manner. The sense of having understood the joke arises when the surprising incongruity can be resolved by consideration of information available elsewhere in the joke or cartoon (Suls, 1972; Ruch, 2001; Ruch and Hehl, 2007). This process, which resembles problem solving, is followed by a positive emotional response (i.e., amusement) that can greatly differ inter-individually (Ruch, 2007). It has been shown that the perception of humor reliably produces a transient psychophysiological response that can be observed in close proximity to the perception of humor (i.e., to the detection of the punch line or the moment of insight). It is indicated by a relative heart rate acceleration in conjunction with increased cardiac output (Lackner et al., in press). The transient cardiovascular activation follows an initial period of cardiac deactivation that can be attributed to stimulus processing (De Pascalis et al., 1995; Lackner et al., in press).

Thus, the cardiovascular response to the perception of humor seems to reflect the effect of the process of insight, which is an activating experience linked to reward and pleasure by itself (Shaw, 1999) plus the additional effect of amusement, which is a strong approach-related emotion involving high arousal (Christie and Friedman, 2004). Related to that, Jaušovec and Bakracevic (1995) demonstrated a sudden increase of heart rate when participants had solved an insight problem. In addition, there is evidence showing that transient activation of the behavioral approach system (produced, for instance, by signals of impending reward or actual pleasure) is accompanied by transient heart rate acceleration, which comes out especially clearly when contrasting it to the response to neutral stimulation (Bradley et al., 2001; Fowles et al., 1982). Further, individuals rating stimuli as more pleasant showed a more pronounced heart rate acceleration (Aupee and Jönsson, 2008). It has also been demonstrated that the transient cardiovascular response to the perception of humor varies inter- and intraindividually according to the level of perceived amusement. That is, the cardiovascular response following the detection of the punch line is more pronounced the more amusement it provokes (Lackner et al., in press).

Against this background, the current study was designed to determine whether EEG asymmetry at the ventrolateral and dorsolateral prefrontal electrode sites, measured in resting conditions, may be related to individual differences in the psychophysiological and behavioral responsivity in the domain of positive affect. The EEG asymmetry at a given time is influenced by both trait and state aspects of asymmetrical cortical activity (Davidson, 1988; Papousek and Schulter, 2006). According to relevant models of laterality research, the trait portion of EEG asymmetry is considered to underlie a specific "affective style" and a heightened predisposition to affective disorders (Davidson, 1998). However, inter-individual differences in resting EEG asymmetry measures at a given time do only qualify as a neurophysiological correlate or substrate of affect-related dispositions or disorders, if they can predict relevant variables assessed in some temporal distance from the EEG recordings (see, e.g., Nusslock et al., 2011; Pössel et al., 2008 for corresponding empirical evidence). Therefore, in the present study the participants' responsivity to the humor was assessed several weeks after the EEG recordings.

Participants were presented with non-verbal humorous cartoons and cardiovascular variables were obtained. After viewing each cartoon, the participants indicated whether they did or did not understand the punch line and rated the cartoons for funniness, and the time it took them to deliver the ratings was recorded. The response latencies to the comprehension ratings are primarily determined by the efficiency of the cognitive-emotional process of detecting the humor (i.e., the easiness of detecting the cartoon's punch lines). The response latencies to the amusement rating may reflect how difficult it is to perceive and judge one's amusement and probably implicate effective emotion regulation (Papousek et al., submitted for publication; Samson et al., 2012). The amusement rating is related to positive emotional responsiveness. In order to examine the transient cardiovascular response to the perception of humor (i.e., to the moment of insight), cardiovascular activation was studied during a time window immediately before the participants indicated having understood the punch line of cartoons, contrasting it to the activation during the processing of non-humorous cartoon-like pictures. As the study was intended to examine the relationship of frontal brain asymmetry to responses to the perception of humor as an individual disposition, healthy participants were tested, excluding confoundations with potential consequences of mental illness or medication.

2. Method

2.1. Participants

Forty-two right-handed university students aged 18 to 36 years (M=23.5, SD=4.5) completed the experiment (22 women, 20 men). Handedness was assessed by a standardized handedness test (Hand Dominance Test; Papousek and Schulter, 1999; Steingrüber and Lienert, 1971). Participants were requested to refrain from alcohol for 12 h and from coffee and other stimulating beverages for 4 h prior to their lab appointment, and to come to the session well rested. No participant reported

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