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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.



## 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 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 using drugs or psychoactive medication and none had participated in an experiment using cartoons before. The study was performed in accordance with the American Psychological Association's Ethics Code and the 1964 Declaration of Helsinki and was approved by the local ethics committee. Participants gave their written consent to participate in the study.

### 2.2. EEG recording and quantification

EEG was recorded from 19 channels according to the international 10–20 system, using a Brainvision BrainAmp Research Amplifier (Brain Products) and a stretchable electrode cap, and was re-referenced to a mathematically averaged ears reference (Hagemann, 2004). According to the research question, the dorsolateral frontal positions F3 and F4 and the ventrolateral positions F7 and F8 were used for the analyses. Horizontal and vertical EOG measures were obtained for identification of ocular artifacts. All data were inspected visually, in order to eliminate intervals in which ocular or muscle artifacts occurred. Power spectra (epoch length 1 s) were averaged across all artifact-free intervals for an individual. Following the common approach in the field, power within the alpha frequency band (8–12 Hz) was used for the analyses. When lateralized effects of hemispheric activity are in the focus of interest, relating data of the left and the right hemisphere by the use of laterality coefficients has several distinct advantages (Coan and Allen, 2004; see also Section 1). We computed EEG laterality coefficients (LC) for each frequency band and position as follows: $LC = ((L - R)/(L + R)) \times 100$. Positive values indicate higher alpha activity in the left than in the right hemisphere (i.e., relatively greater right hemisphere cortical activity). The calculation of LC has a long tradition in laterality research, because it separates the variance in asymmetry from the variance in general magnitude (e.g., Porac and Coren, 1981). In EEG studies, this asymmetry ratio is equivalent to another common metric (lnL – lnR), with which it is virtually perfectly correlated (Davidson, 1988; Papousek and Schulter, 2002). We prefer LC, because it allows the most straight-forward interpretation, and data of different studies, different frequency bands, and locations can most easily be compared (Pivik et al., 1993).

### 2.3. Humor paradigm

The stimulus material consisted of three types of cartoons (puns, semantic jokes, and jokes requiring mentalizing) as well as non-humorous pictures serving as a control condition. They were used in previous studies (e.g., Papousek et al., submitted for publication; Samson and Hegenloh, 2010; Samson et al., 2008, 2012). Being not relevant to the research question of the present study, the three types of cartoons were not analyzed separately. The non-humorous control pictures were cartoon-like pictures containing an incongruity which could not be resolved meaningfully, that is, they did not contain a punch line. All pictures were low in aggressive, violent, and sexual content.[2] During the experiment, a total of 96 pictures were presented, divided into three blocks of 32 pictures each. Within each block, the pictures (24 cartoons and 8 non-humorous pictures) were presented in random order. A 10 min break was provided between the blocks. The order of blocks was counterbalanced.

#### 2.3.1. Behavioral indicators of humor processing

During the humor paradigm, the participants indicated via mouse click whether they had or had not understood the punch line of the cartoon (comprehension rating) and rated the funniness of each cartoon from 1 (not funny) to 6 (very funny; amusement rating). The computer program also calculated the response latencies to the comprehension ratings (starting from the onset of the cartoon) and amusement ratings (starting from the onset of the rating scale). On average, $M = 66.5$ ($SD = 6.1$), i.e., 92 per cent of the punch lines were understood. As there was only very little variance in the answers to the comprehension questions, they were not further analyzed. The amusement ratings and the response latencies to the amusement and to the comprehension ratings were averaged across all items of all blocks. Residualized scores were calculated, in order to control for general individual differences in response tendencies and response speed (e.g., Fazio, 1990). This was done by conducting linear regressions using the scores of the control pictures to predict those of the cartoons (see also Samson et al., 2012). The use of residualized scores ensured that the analyzed residual variability was specific to the participants' evaluation of the experience of humor and accompanying feelings of amusement, as opposed to the evaluation of any pictures or recognition of any incongruence.

### 2.4. Recording and quantification of cardiovascular measures

Continuous hemodynamic monitoring of blood pressure (BP; sampling rate = 100 Hz, $BP_{range} = 50–250$ mmHg, $\pm 5$ mmHg), heart rate (HR; 3-lead electrocardiography (ECG), sampling rate = 1 kHz, $f_{cut\text{-}off} = 0.08–150$ Hz) and thoracic impedance (sampling rate = 100 Hz, $Z_{0,\,range} = 10–75\ \Omega$, $dZ/dt = \pm 10\ \Omega/s$) was carried out with the Task Force Monitor® (TFM®; CNSystems, Graz, Austria). Continuous blood pressure was derived from the finger using a refined version of the vascular unloading technique and corrected to absolute values with oscillometric blood pressure measurement on the contralateral upper arm by the TFM® (Fortin et al., 2006b). Electrodes were placed at the neck and thoracic regions, the latter specifically at the midclavicular line at the xiphoid process level (Fortin et al., 2006a).

For heart rate, blood pressure and the variables related to impedance cardiography beat-to-beat values computed by the TFM® were used. Thoracic impedance $Z_0(t)$ and impedance variation $dZ(t)/dt$ were used to calculate beat-to-beat stroke volume based on an improved Kubicek approach and cardiac output (Gratze et al., 1998). To obtain time series with equidistant time steps for the investigation of transient responses, the beat to beat values were resampled to 4 Hz using piecewise cubic spline interpolation. Artifact handling of beat to beat values was done semi-automatically, using the time series with equidistant time steps after resampling to 4 Hz, and physiological limits as well as the maximal percentage of change relative to the standard deviation of the signal as criteria. The rate of invalid data was very low (on average 0.2%). Single artifacts were replaced by interpolation.

#### 2.4.1. Cardiovascular responses to the perception of humor

Following Lackner et al. (in press), data in the time window beginning 0.5 s before picture onset and ending 6 s after picture onset were used for the calculation of the transient cardiovascular responses to the perception of humor. In the first step, for each of the 96 pictures cardiovascular changes following the presentation of the picture were calculated relative to the mean of the 0.5 s frame preceding the picture onset. In the second step, these relative changes were averaged across trials, separately for cartoon trials and trials with presentation of non-humorous control pictures (see Fig. 1). In the third step, average values across the 0.5 s frame immediately preceding the participant's response indicating having understood the punch line were calculated (for cartoon trials). This was done using a sample rate of 8 Hz. Data from the same 0.5 s time frame were used to calculate the respective scores for the control trials (see Fig. 1). Finally, for all cardiovascular variables, the individual's response to the perception of humor was computed as the difference between the score for cartoon trials minus the score for control trials ("Contrasted Transient Response"). Higher positive values indicate a more pronounced cardiovascular response to the perception of humor. The scores were residualized for the scores in the control trials by using linear regression, in order to eliminate potential influences of individual differences in the basic response to the processing of pictures. This procedure was shown to result in valid indicators of the response to the perception of humor (Lackner et al., in press).

### 2.5. Additional measures

In order to evaluate the effects of brain asymmetry on the perception of humor independently from current symptoms of depression, the CES-D was applied (German version, Hautzinger and Bailer, 1993). It is comprised of 20 items referring to mood and attributions over the past week. It is particularly suitable to measure sub-clinical depressive experiences in the general population (Wood et al., 2010). In addition, the participants were asked after each block of the humor paradigm how much efforts they had made to accomplish the task (17-point rating scale, from 1 "not at all" to 17 "extremely").

### 2.6. Procedure

Data were obtained in two separate sessions. The humor paradigm was applied 16 to 24 weeks after the EEG recording.

After some questions on demographic data and performance of the hand dominance test, participants were seated in an acoustically and electrically shielded examination chamber, and electrodes were attached. EEG was recorded in a 2 min rest period with closed eyes. A closed-eyes condition was chosen to be able to link the results to previous research on EEG asymmetries and affective flexibility (Papousek et al., 2012). There is evidence that small variations in recording conditions such as open vs. closed eyes can cause considerable shifts in EEG asymmetries (Papousek and Schulter, 1998). Previous analyses had confirmed that internal consistency reliabilities of a 2 min rest period with closed eyes are virtually identical to those reported for the commonly used average of several alternating closed- and open-eyes blocks (Papousek and Schulter, 2002; Reid et al., 1998; Sutton and Davidson, 1997; Tomarken et al., 1992).

In session two, the participants were tested in the same examination room. After the CES-D was administered, the participants received instructions for the task and were given sample cartoons and the required responses. Each cartoon was presented for 6 s on a computer screen, along with two buttons at the bottom of the screen ("not understood", "understood"). Participants were required to indicate for each picture via mouse click whether they had or had not understood the punch line of the cartoon and were instructed to click the respective button as soon as they had understood the punch line or were sure that they did not understand it (using their preferred, i.e., right hand). After presentation of each cartoon, a scale appeared for 4 s on which the participants rated via mouse click the funniness of each cartoon.

[2] Please see Samson et al. (2008, 2012) for examples of humorous cartoons and non-humorous pictures.

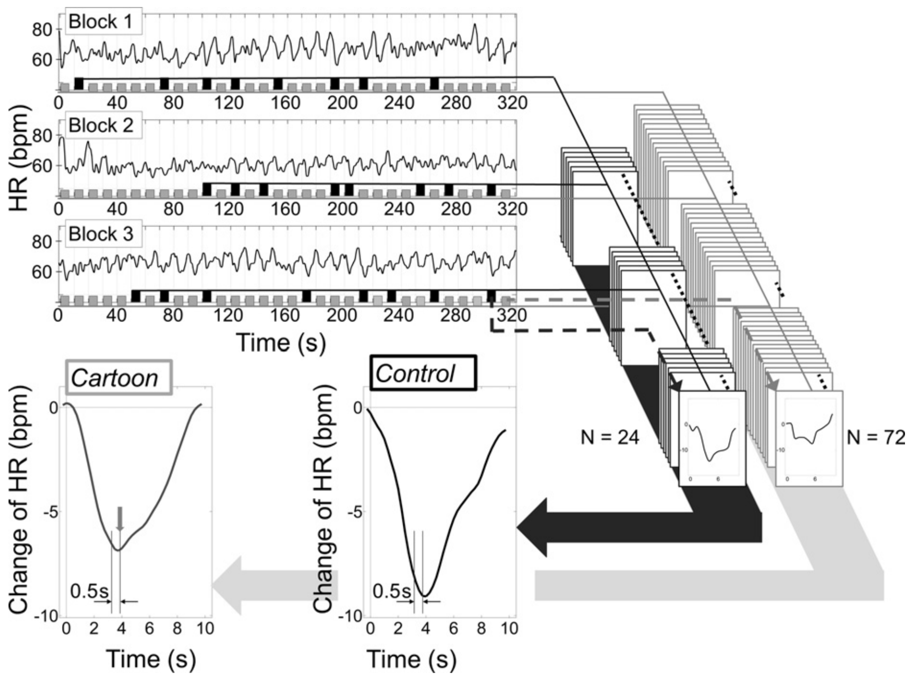


**Fig. 1.** Calculation of transient cardiovascular responses to the perception of humor.
The upper panel shows the time course of the resampled heart rate (4 Hz) of a participant during the three blocks of 32 trials each. The gray squares indicate periods of cartoon presentation (6 s each, 72 trials in total), the black squares mark periods during which non-humorous control pictures were presented (6 s each, 24 trials in total). For the calculation of the transient cardiovascular responses to the perception of humor, data in the time frame beginning 0.5 s before and ending 6 s after picture onset were used. Cardiovascular changes following the presentation of the picture were calculated relative to the mean of the 0.5 s frame preceding the picture onset. These relative changes were averaged across trials, separately for cartoon trials (gray path) and control trials (black path). Average values across the 0.5 s frame immediately preceding the participant's response indicating having understood the punch line in cartoon trials were calculated (gray arrow, lower left panel). Data of the same 0.5 s time interval were selected from the data of the control trials (lower right panel). The difference between the score for cartoon trials minus the score for control trials was used to indicate the individual's response to the perception of humor (Lackner et al., in press).

In both sessions the technical equipment and the experimenter were located outside the examination chamber, and the participants were monitored through a one-way window and an intercom.[3]

### 2.7. Data analysis

To evaluate whether the EEG alpha asymmetry at the ventrolateral or the dorsolateral frontal positions may predict the participants' responses in the humor paradigm, hierarchical multiple regression analyses were performed. The cardiovascular or the behavioral variables obtained in the humor experiment were used as the dependent variables. Sex, depression (Step1) and either the ventrolateral or the dorsolateral EEG asymmetry (Step 2) were entered as the predictors. A significant $F_{change}$ test indicates that the baseline EEG asymmetry explained a significant amount of variance of the behavioral or cardiovascular response in the humor paradigm, independently of potential influences of sex or depression. $\Delta R^2$ indicates the amount of variance that the EEG asymmetry could explain independently of variance that might be explained by sex or depression.

Results are reported in terms of cortical activation: "Left > Right" indicates relatively greater left than right sided cortical activity (i.e., relatively lower left than right sided EEG alpha values, because alpha power is inversely related to cortical activity).

## 3. Results

### 3.1. Cardiovascular responses to the perception of humor

A multivariate repeated measures analysis indicated significant effects of the perception of humor (i.e., a significant difference between humorous cartoons and non-humorous control pictures; $F(5,37) = 2.4$, $p = .05$). Univariate test showed that the difference was significant for heart rate ($F(1,41) = 6.1$, $p < .05$, $\eta_p^2 = .13$), diastolic blood pressure ($F(1,41) = 6.4$, $p < .05$, $\eta_p^2 = .14$), and cardiac output ($F(1,41) = 6.5$, $p < .05$, $\eta_p^2 = .14$), but not for systolic blood pressure ($F(1,41) = .4$, ns.) and stroke volume ($F(1,41) = .19$, ns.). The average transient heart rate response to the perception of humor (difference humorous cartoons minus non-humorous control pictures) was $M = +0.47$ bpm (SD = 1.5). Diastolic blood pressure increased on average by $M = +0.42$ mmHg (SD = 1.1). Cardiac output increased on average by $M = +0.04$ l/min (SD = .1).

#### 3.1.1. Ventrolateral asymmetry

A relatively stronger Left > Right resting asymmetry was associated with relatively greater heart rate responses ($F_{change}(1,38) = 7.9$, $p < .01$; $\beta = -.44$, $\Delta R^2 = .17$) and cardiac output ($F_{change}(1,38) = 9.2$, $p < .005$; $\beta = -.46$, $\Delta R^2 = .19$) responses to the humor, after sex and depression were controlled. No effects of the ventrolateral asymmetry were observed for systolic blood pressure ($F_{change}(1,38) = .02$, ns.; $\beta = -.02$, $\Delta R^2 = .0$), diastolic blood pressure ($F_{change}(1,38) = 3.3$, ns.; $\beta = -.28$, $\Delta R^2 = .07$), and stroke volume ($F_{change}(1,38) = .03$, ns.; $\beta = .03$, $\Delta R^2 = .0$). Sex and depression did not explain a significant amount of variance of any of the cardiovascular variables. See Fig. 2 for a scatter plot of EEG asymmetry and heart rate responses.

#### 3.1.2. Dorsolateral asymmetry

Results for the resting asymmetry at the dorsolateral prefrontal electrodes were generally weaker than those for the ventrolateral asymmetry, and were not significant for any of the cardiovascular variables (heart rate $F_{change}(1,38) = 2.6$, ns.; $\beta = -.25$, $\Delta R^2 = .06$; cardiac output $F_{change}(1,38) = 3.6$, $p = .07$; $\beta = -.29$, $\Delta R^2 = .09$; systolic blood pressure $F_{change}(1,38) = .6$, ns.; $\beta = -.12$, $\Delta R^2 = .01$; diastolic blood pressure $F_{change}(1,38) = 3.1$, $p = .09$; $\beta = -.26$, $\Delta R^2 = .07$; stroke volume $F_{change}(1,38) = .1$, ns.; $\beta = .02$, $\Delta R^2 = .0$).

[3] Additional data were obtained for purposes not related to the present research question.

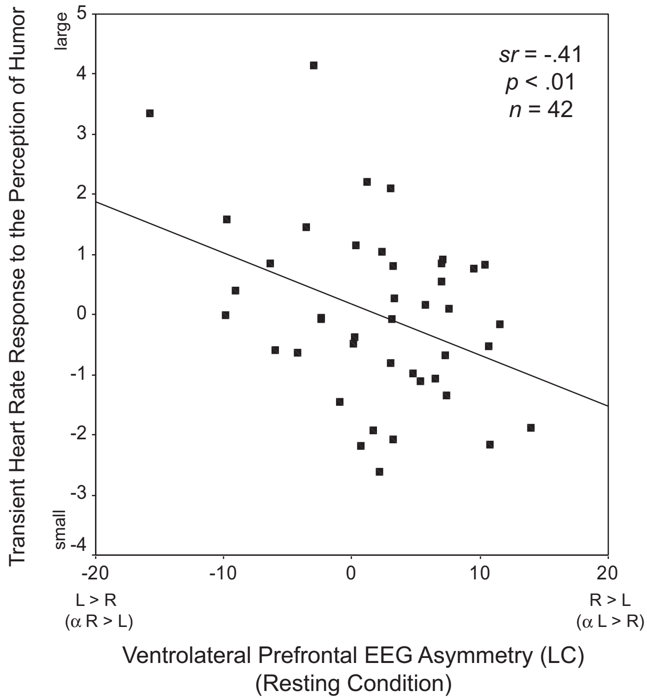


**Fig. 2.** Scatter plot of EEG asymmetry and heart rate responses.

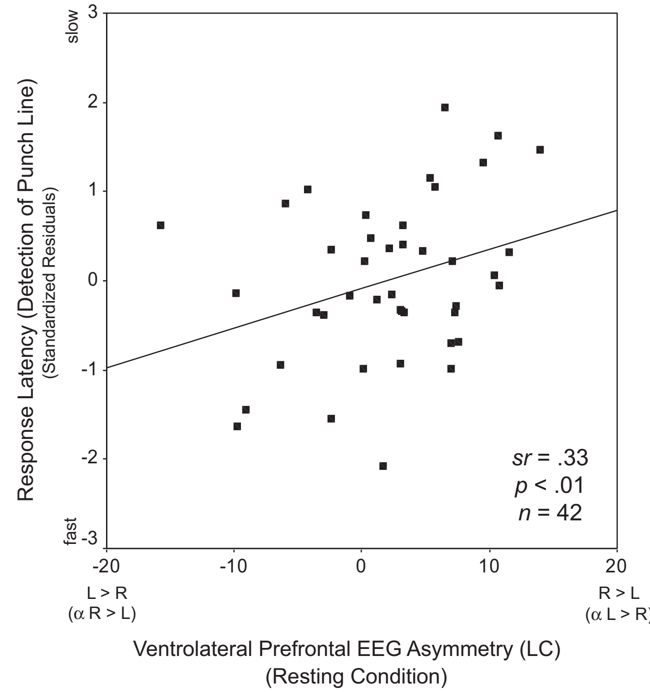


**Fig. 3.** Scatter plot of EEG asymmetry and response latencies to the comprehension rating.

### 3.2. Behavioral indicators of humor processing

#### 3.2.1. Ventrolateral asymmetry

Independently from sex and depression, the resting asymmetry at the ventrolateral electrodes predicted the time it took the participants to indicate having detected the punch line in the cartoons ($F_{change}$(1,38) = 4.7, $p$ < .05; $\beta$ = .35, $\Delta R^2$ = .11). A stronger Left > Right asymmetry in the ventrolateral frontal cortex was associated with faster responses. Relatively higher left than right hemispheric activity also predicted faster responses to the amusement ratings ($F_{change}$(1,38) = 5.3, $p$ < .05; $\beta$ = .37, $\Delta R^2$ = .12). No significant effect was observed for the reported levels of amusement ($F_{change}$(1,38) = .5, ns.; $\beta$ = −.12, $\Delta R^2$ = .01). Fig. 3 shows the scatter plot of EEG asymmetry and response latencies to the comprehension rating.

#### 3.2.2. Dorsolateral asymmetry

Neither the detection of the punch line ($F_{change}$(1,38) = 1.6, ns.; $\beta$ = .20, $\Delta R^2$ = .04), nor the reported levels of amusement ($F_{change}$(1,38) = .0, ns.; $\beta$ = .01, $\Delta R^2$ = .0), nor the response latencies to the amusement ratings ($F_{change}$(1,38) = .6, ns.; $\beta$ = .13, $\Delta R^2$ = .02) showed associations with the asymmetry at the dorsolateral frontal electrodes.

Neither sex nor depression was a significant predictor of any of the behavioral indicators of humor processing.

### 3.3. Supplemental analyses

The intercorrelations among the behavioral variables were: response latency (comprehension) – amusement $r$ = −.35 ($p$ < .05), response latency (comprehension) – response latency (amusement) $r$ = .48 ($p$ < .001), amusement – response latency (amusement) $r$ = −.07 (ns.). The prefrontal EEG asymmetries were not correlated with the self-report rating of how much efforts the participants had made to accomplish the task (averaged across the three blocks; ventrolateral: $r$ = −.09, $p$ = .57; dorsolateral: $r$ = −.10, $p$ = .52). The amount of artifact free EEG data (number of seconds) was not significantly correlated with ventrolateral ($r$ = −.14, $p$ = .37) or dorsolateral asymmetry ($r$ = −.11, $p$ = .47) nor with any of the cardiovascular measures or behavioral measures in the humor paradigm (all $ps$ > .10). Body mass was not correlated with the cardiovascular responses to the perception of humor (contrasted transient responses, all $ps$ > .50).

## 4. Discussion

The present study demonstrated that the EEG asymmetry in the prefrontal cortex, measured in resting conditions, was related to individual differences in the immediate response to the perception of humor. Relatively greater resting activity in the left than right prefrontal cortex at the ventrolateral positions was associated with more pronounced cardiac responses when participants had detected the punch line of cartoons. In addition, participants with a Left > Right asymmetry at rest took less time to detect the punch line and indicated their level of amusement more quickly. Notably, the EEG was recorded several weeks before the behavioral humor paradigm, that is, frontal brain asymmetry prospectively predicted an individual's response to the perception of humor.

A clear response to the perception of humor was observed for heart rate and cardiac output, whereas there were no significant effects on stroke volume and (systolic) blood pressure. This is in line with a recent study in which the time course of the cardiovascular response before and after the detection of the punch line in cartoons was analyzed in detail (Lackner et al., in press) and can be explained by the ability of the heart rate to respond immediately on a beat to beat basis (see also, e.g., Ruiz-Padial et al., 2011). The lacking effect on the stroke volume suggests that the increase in cardiac output is related to the heart rate acceleration (Lackner et al., in press). Correspondingly, effects of resting EEG asymmetry were also found for heart rate and cardiac output responses only. The correlation of relatively greater left than right prefrontal brain activity with a greater responsivity in the domain of positive affect is consistent with theoretical accounts proposing that left prefrontal regions are involved in an individual's propensity to engage in appetitively motivated behavior and to experience approach-related affect (Davidson, 2004).

The behavioral data obtained during the humor experiment add further information on which components of the response are linked to the asymmetry of prefrontal brain activity. First, the shorter response latencies to the comprehension question in participants with a relatively stronger Left > Right asymmetry indicate that these individuals detected the cartoon's punch lines more easily. The perception of humor involves viewing what is originally perceived in one (often serious) sense from a different perspective, in order to detect the incongruity between a concept (or expectation) and the observed object or situation (Suls, 1972; Ruch, 2001). That is, it requires sensitivity to detect non-prepotent solution candidates and cognitive switching from more common ideas or concepts to ones that are less apparent (Weiss et al., in press). These processes resemble those occurring in the context of insight during problem solving when individuals initially focus on a dominant but incorrect association and need to overcome this impasse and switch to the correct solving strategy to be able to reach a sudden understanding of the solution (Bowden et al., 2005). The comprehension and appreciation of humor additionally requires the integration of these cognitive processes with positive affective responsiveness (Ruch, 2001; Shammi and Stuss, 2003). Thus, in individuals with relatively stronger Left > Right prefrontal activity in resting conditions, the cognitive processes activated for detecting the humor seem to be more effective, perhaps specifically in interaction with the rewarding outcome (i.e., the pleasant experience of amusement).

This consideration is in line with evidence of important involvement of lateral prefrontal regions in flexible cognition, specifically when task performance requires overriding a highly activated or prepotent representation. The left hemisphere seems to be more important for these processes than are homologous regions in the right hemisphere (Henry and Crawford, 2004; Jahanshani et al., 2000; Jonides et al., 2000; Jonides and Nee, 2006; Joppich et al., 2004; Schneider et al., 2004). In addition, it has been suggested that a Left > Right asymmetry of activity in the prefrontal cortex may predispose an individual to information processing biases toward positive cues: Relatively greater left prefrontal resting activity was associated with greater responsiveness to reward-related cues, that is, with a greater propensity to modulate behavior as a function of incentives (Pizzagalli et al., 2005).

The association of relatively greater left than right hemisphere activity in resting conditions with shorter response latencies to the amusement ratings may be more difficult to explain. The response latencies to the amusement ratings are related to the easiness of perceiving and judging one's amusement (Samson et al., 2012). There is some evidence that this implicates effective emotion regulation. During viewing cartoons, also negative feelings may arise to a certain extent, because most jokes (also those that are not aggressive) involve a victim (the butt of a joke) who, for instance, has a false belief. This is associated with negative emotions that the viewer may infer and adopt to a certain extent (Moran, 1996). (Down)-regulation of these emotions may facilitate the perception and judgment of one's level of positive affect. The present study does not provide explicit empirical evidence for this interpretation, but other evidence suggested that higher levels of negative affect occurring during viewing the cartoons may hamper the experience of amusement and, therefore, may slow down the responses to the amusement ratings (Papousek et al., in press; Samson et al., 2012). Results of a recent brain imaging study demonstrating that not only brain circuits related to emotion perception but also circuits related to emotion regulation contributed to the affective response to humor in cartoons may further support this interpretation (Kohn et al., 2011).

Taken together, the shorter response latencies to the comprehension question and the amusement rating in individuals with a greater Left > Right prefrontal asymmetry at rest go nicely with the concept of flexibility, which implies the selection of appropriate and the inhibition of inappropriate processes (Thayer and Friedman, 2002). Thus, the findings of the present study can be well aligned with previous evidence suggesting a relation of the prefrontal resting asymmetry to affective flexibility (Papousek et al., 2012). Affective flexibility refers to adaptive variability encompassing emotional responsivity to an emotional event and effective emotional regulation (Papousek et al., 2012; Waugh et al., 2008).

As more pronounced transient cardiac responses to the perception of humor are correlated with higher levels of perceived amusement (Lackner et al., in press), it may also be concluded that relatively greater left than right hemisphere resting activity in the prefrontal cortex is associated with greater positive emotional responsiveness. However, this is not supported by the amusement ratings which did not show a relation to the individual's EEG asymmetry. Prefrontal brain asymmetry may be associated with a propensity to show approach-related behavioral tendencies in response to specific cues but not so much with the degree of hedonic tone (in this case amusement), as was suggested on the basis of other empirical findings (Pizzagalli et al., 2005). However, it should also be noted that the amusement rating is the only self-reported variable in the behavioral humor paradigm and, thus, could be weaker than the more objective cardiovascular variables and response times, more prone to demand characteristics or more easily be influenced by other personality characteristics.

Although the present findings can be well aligned with the literature, research on joke comprehension and appreciation traditionally emphasizes the importance of right (rather than left) hemisphere functions (e.g., Coulson and Williams, 2005; Marinkovic et al., 2011). On the other hand, most magnetic resonance imaging studies suggested more left hemisphere involvement in humor processing (for review see Samson et al., 2008). Discrepancies may be due to fundamental differences in research questions and study designs. Whereas other studies examined various cognitive subprocesses during the processing of jokes, the point in the present study was whether the trait portion of asymmetrical prefrontal activity, observed in resting conditions, may predict an individual's response to the perception of humor, that is, when the processing of the humorous stimuli had come to a successful and rewarding end.

Finally, it should be noted that two possible sources of artifacts can be excluded. Firstly, the findings for the response latencies cannot be explained by general individual differences in response speed, because residualized scores controlling for the scores of the non-humorous control pictures were used. This ensured that the analyzed variability was specific to the participants' responses to the perception of humor. Secondly, the specific calculation of the transient cardiovascular responses to the perception of humor rules out that they might have been influenced by the response latencies to the comprehension question (see Lackner et al., in press).

A limitation of the study is that the phase of the menstrual cycle was not controlled in the female participants, which might have introduced some error variance because hormonal fluctuations may influence activity patterns in the brain (Hausmann et al., 2002; Hwang et al., 2008). However, as the time intervals between the two sessions varied randomly, a systematical influence on the results can be excluded.

In summary, the present study supports 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. A more pronounced Left > Right asymmetry in the ventrolateral prefrontal cortex, measured in baseline conditions, predicted faster detection of humor, more pronounced cardiac responses to the perception of humor, and more accessible internal positive affective states. This pattern of responding may be relevant in the context of affective disturbances, for instance, to the prediction of illness outcomes (Rottenberg et al., 2002).

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