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Models of hemispheric specialization in facial emotion perception - a reevaluation

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Abstract

A considerable amount of research on functional cerebral asymmetries (FCAs) for facial emotion perception has shown conflicting support for three competing models: (i) the Right Hemisphere Hypothesis, (ii) the Valence-Specific Hypothesis, and (iii) the Approach/Withdrawal model. However, the majority of studies evaluating the Right Hemisphere or the Valence-Specific Hypotheses are rather limited by the small number of emotional expression used. In addition, it is difficult to evaluate the Approach/Withdrawal hypothesis due to insufficient data on anger and FCAs. The aim of the present study was (a) to review visual half field (VHF) studies of hemispheric specialization in facial emotion perception and (b) to reevaluate empirical evidence with respect to all three partly conflicting hypotheses. Results from the present study revealed a left visual field (LVF)/right hemisphere advantage for the perception of angry, fearful, sad, and surprise facial expression and a right visual field (RVF)/left hemisphere advantage for the perception of happy expressions. Thus, FCAs for the perception of specific facial emotions do neither fully support the Right Hemisphere Hypothesis nor the Valence-Specific Hypothesis or the Approach/Withdrawal model. A systematic literature review, together with the results of the present study, indicate a consistent LVF/right hemisphere advantage only for a subset of negative emotions which included anger, fear and sadness, rather suggesting a “negative (only) valence model”.

Introduction

There has been considerable evidence supporting the idea that the left and the right hemispheres are differentially involved in the perception of emotions (Adolphs, Jansari, & Tranel, 2001; Ahern & Schwartz, 1979; Harmon-Jones, 2004; Wedding & Stalans, 1985), which is relatively consistent across different cultures (Eviatar, 1997).

However, far from been unanimous, studies on FCAs for facial emotion perception have led to three partly conflicting models: (i) the Right Hemisphere Hypothesis (Borod et al., 1998), (ii) the Valence-Specific Hypothesis (Adolphs et al., 2001; Ahern & Schwartz, 1979; Wedding & Stalans, 1985), and (iii) the Approach/Withdrawal model (Harmon-Jones, 2004). The first hypothesis posits that all emotions are preferentially processed by the right hemisphere. The second, Valence-Specific Hypothesis proposes left hemisphere specialization for processing positive emotions (e.g., happiness, surprise) and right hemisphere dominance for processing negative emotions (e.g., anger, fear, disgust, sadness). Finally, the Approach/Withdrawal model, considered as another version of the Valence-Specific Hypothesis, proposes that FCAs are organized according to approach and withdrawal motivation (Harmon-Jones, 2004). Approach motivation is related to a drive of the individual toward the environmental stimuli which has been proposed to be primarily processed by the left hemisphere. On the other hand, withdrawal behaviors leading the individual away from the environment are associated with right hemisphere processing. The two versions of the Valence-Specific Hypothesis overlap with respect to the majority of emotions. However, both versions differ substantially with respect to anger. Whereas the original Valence-Specific Hypothesis considers anger as a negative emotion arising from events that are unpleasant or undesired (Harmon-Jones, 2004), the Approach/Withdrawal Hypothesis categorizes anger as an approach tendency because it implies a goal blockage disruption (Berkowitz, 1993; Depue & Zald, 1993). Therefore anger has crucial implications for differentiating between the two versions of the Valence-Specific Hypothesis. FCAs in valence-specific processing have also been reported in other species, suggesting a possible evolutionary adaptive principle. For example, in rats the right hemisphere controls fear responses (Robinson, 1985) and a right eye and left hemisphere guidance is involved in prey-catching in a wide variety of birds species, but also fishes, reptiles and toads (MacNeilage, Rogers, & Vallortigara, 2009). Although the Approach/Withdrawal model directly relates to emotional experience, it is possible that facial emotion perception might activate neural networks that are associated with emotional experience. This might particularly be the case for the amygdala which has been associated with greater right compared to left-sided activation during LVF presentation of fearful faces (Noesselt, Driver, Heinze, & Dolan, 2005; Hung et al., 2010). If FCAs for facial emotion perception depend on motivational direction, then one would expect a left hemisphere advantage for happiness, surprise, and anger (approach motivation), and a right hemisphere advantage for sadness, fear and disgust (withdrawal motivation).

The right hemisphere and the valence-specific models in facial emotion perception have been evaluated by a large number of studies using the VHF technique (Alves, Aznar-Casanova, & Fukusima, 2009; Burton & Levy, 1989; Buchtel, Campari, DeRisio, & Rotal, 1978; Hugdahl, Iversen, Ness, & Flaten, 1989; Hugdahl, Iversen, & Johnsen, 1993; Jansari, Rodway, & Goncalves, 2011; McKeever & Dixon, 1981; Landis, Assal, & Perret, 1979; Ley & Bryden, 1979; Reuter-Lorenz & Davidson, 1981; Rodway, Wright, & Hardie, 2003; Safer, 1981; Stafford & Brandaro, 2010; Strauss & Moscovitch, 1981; Suberi & McKeever, 1977; Van Strien & Van Beek, 2000). The VHF paradigm is an experimental technique that relies on the visual projections from the right and left hemiretina of the eyes to the right and left cerebral hemispheres, respectively. Thus, an emotional face briefly presented in the LVF is finally projected to the contralateral right hemisphere and vice versa. Although both hemispheres are involved in emotional processing, the relative differences in emotional face perception can be detected by differences in accuracy and/or response times for emotional faces presented in the LVF (corresponding to the right hemisphere) relative to the performance following RVF (corresponding to the left hemisphere) stimulation. Among the studies evaluating both left and right handers (e.g. Rodway et al., 2003; Van Strien & Van Beek, 2000), no differences in FCAs for facial emotion perception have been reported, suggesting that right hemisphere advantage in facial emotion perception is relatively independent from handedness.

Although FCAs are measured under experimental conditions such as the VHF paradigm, fMRI studies investigating the functional brain organization almost always report FCAs in brain activation following foveal presentation of emotional stimuli (e.g. Blair, Morris, Frith, Perrett, & Dolan, 1999; Morris et al., 1998; Gauthier, Behrmann, & Tarr, 1999). Similar FCAs have been found in other modalities, for example in a dichotic listening task which required participants to recognize a particular emotional tone of voice (e.g. Grimshaw, Kwasny, Covell, & Johnson, 2003). Given that FCAs in emotion perception can be observed across modalities, this suggests a general mechanism in the functional brain organization for emotion processing.

Several of these VHF studies have shown results favoring the Right Hemisphere model in facial emotion perception (Alves et al., 2009; Buchtel et al., 1978; Hugdahl et al., 1989, 1993; McKeever & Dixon, 1981; McLaren & Bryson, 1987; Landis et al., 1979; Ley & Bryden, 1979; Safer, 1981; Strauss & Moscovitch, 1981; Suberi & McKeever, 1977). Specifically, Safer (1981) revealed higher accuracy rates for recognizing facial emotions presented in the left visual field (LVF) using the six basic emotions. Similarly, Alves, Aznar-Casanova, & Fukusima, (2009) tested five groups of healthy controls with an assigned emotional target of happy, surprise, fearful, sad or neutral expression and asked participants to indicate the VHF where the target was presented. Alves, Aznar-Casanova, & Fukusima, (2009) found faster responses to LVF presentations only for happy and fearful faces but not for sad and surprise stimuli. However, the authors interpreted their finding as support for the Right Hemisphere Hypothesis (Alves et al., 2009). Likewise, a series of other studies, found faster responses and/or higher accuracy for the perception of emotional faces presented to the LVF. Although these studies only included three (Landis et al., 1979; McKeever & Dixon, 1981; Strauss & Moscovitch, 1981; Suberi & McKeever, 1977) or two emotions (Buchtel et al., 1978; Hugdahl et al., 1993; McLaren & Bryson, 1987), the results were interpreted as support for the Right Hemisphere Hypothesis.

Moreover, the evidence is additionally limited by the fact all these studies used different paradigms including the match-to-sample, emotion recognition, and same-different paradigms. Moreover, the majority of studies did not differentiate between specific emotions but analyzed them in combination, which makes it difficult to evaluate whether the valence hypotheses are perhaps the better approach. The study of Alves, Aznar-Casanova, & Fukusima, (2009) is one of the few VHF studies that differentiated between positive and negative emotion perception. However, their results clearly favoring the Right Hemisphere Hypothesis were restricted to happy and fearful emotions. Moreover, with only a few exceptions (e.g. Alves et al., 2009), the majority of studies reporting a general right hemisphere advantage did not include neutral faces as a control condition. Therefore it cannot be ruled out that a general right hemisphere superiority for emotional face processing was promoted by a general right hemispheric advantage for face processing. In fact, there is extensive evidence from VHF studies, functional neuroimaging, and studies on patients with right hemispheric lesions (e.g., Bentin & Deouell, 2000; Bourne & Hole, 2006; Marotta, McKeeff, & Behrmann, 2002) that the right hemisphere is dominantly involved in face perception regardless of the emotional valence of the face stimuli.

As already mentioned above, there is also evidence supporting a differential involvement of the two hemispheres in processing specific emotions in terms of valence (e.g., Jansari et al., 2011; Rodway et al., 2003; Stafford & Brandaro, 2010). There are three studies that found a valence-specific laterality effect with a LVF advantage for negative emotions and a RVF advantage for positive emotion corresponding to the right and left hemisphere, respectively (Jansari et al., 2011; Rodway et al., 2003; Stafford & Brandaro, 2010). These three studies used facial expressions of the six basic emotions, presented simultaneously in the left and right VHF with an emotion label presented centrally and above the faces. Participants were asked to identify the emotional face matching the label (Jansari et al., 2011; Rodway et al., 2003; Stafford & Brandaro, 2010). In Stafford and Brandaro (2010), the valence-specific laterality finding was restricted to ‘surprise’ and ‘anger’, considered as positive and negative emotions, respectively. A similar valence-specific laterality effect, with faster reaction times for negative emotions in the LVF and positive emotions in the RVF was reported by a VHF study that used the four specific emotions of sadness, delight, anger and content (Burton & Levy, 1989). Finally, other VHF-studies found faster responses to happy and sad emotions presented to the RVF and LVF, respectively; but no further emotions were included (Davidson, Mednick, Moss, Saron, & Schaffer, 1987; Reuter-Lorenz & Davidson, 1981; Reuter-Lorenz, Givis, & Moscovitch, 1983).

Although some of these studies partly support the Valence-Specific Hypothesis evaluating the six basic emotions (Jansari et al., 2011; Rodway et al., 2003; Stafford & Brandaro, 2010), all of them used a task which asks participants to match emotional facial expressions to a verbal label and thus it cannot be ruled out that hemispheric specialization for emotional face processing was confounded by language. Consequently the valence-specific laterality effect might be confounded by preferential involvement of the language-dominant left hemisphere. Regardless of this limitation, the only study analyzing FCAs for six basic emotions found a valence-specific effect only for surprise and anger (Stafford & Brandaro, 2010). The remaining VHF studies supporting the Valence Specific-Hypothesis used a smaller number of specific emotions and found that only the perception of happy and sad emotions supported the valence model (Davidson et al., 1987; Reuter-Lorenz & Davidson, 1981; Reuter-Lorenz et al., 1983). Considering the above mentioned limitations of all these studies, the claim that FCAs for facial emotion perception account for the Valence-Specific model might be compromised.

The majority of studies examining the Approach/Withdrawal Hypothesis in normal participants have focused on the experience or expression of emotion (e.g., Davidson, Ekman, Saron, Senulis, & Friesen, 1990; Davidson & Fox, 1982). To the best of our knowledge only one recent study has examined the Approach/Withdrawal model for perception of emotional faces in normal participants (Alves et al., 2009). Five groups of healthy controls were tested with an assigned emotional target of happiness, sadness, surprise, fear, or neutral (Alves et al., 2009). The study used an emotion recognition task presenting two facial expressions, one emotional and one neutral in either visual field. Participants were asked to identify the side of the emotional target. The analyses for specific facial expressions showed shorter response times for happy and fearful expressions in the LVF, but no VHF effect for surprise or sad expressions. Interestingly, Alves, Aznar-Casanova, & Fukusima, (2009) also found shorter response times for neutral faces presented in the RVF. In particular the finding of a LVF advantage and the lack of FCAs for the perception of fearful and sad faces, respectively, did not support either of the valence hypotheses. Moreover, the Approach/Withdrawal model could not be assessed due to the lack of angry faces, the only emotional expression that allows differentiating between both versions of the valence hypotheses. Although support for the Right Hemisphere Hypothesis was assumed on the basis of the LVF advantage for happy and fearful expressions, this finding does not fully support the model's prediction of a right hemisphere processing for all emotions.

As discussed above, the majority of studies evaluating the Right Hemisphere or the Valence-Specific Hypotheses are rather limited by the small number of emotional expression used. Additionally, not enough data is available on anger and FCAs, which makes it difficult to decide whether the Approach/Withdrawal hypothesis might account for FCAs in emotion perception. The present VHF study aims to test all three partly conflicting hypotheses by presenting Ekman-Friesen faces of all six basic emotions (and emotionally neutral faces).

Methods

Participants

Fifty neurologically healthy participants (25 women, 25 men) participated in this study. The mean age for women was 29.56 years (SD = 3.22, range: 25–35 years) and 30.44 years (SD = 3.44, range: 25–36 years) for men. Ethnicity of all 50 participants was Caucasian (i.e., the same as the emotional faces used by Ekman and Friesen (1976). All participants were right-handed, as determined by the Edinburgh Handedness Inventory (EHI; Oldfield, 1971). The laterality quotient (LQ) provided by this test is calculated as $LQ = [(R - L)/(R + L)]/100$, resulting in values between

−100 and +100. Positive values indicate right-handedness, while negative values indicate left-handedness. Women had a mean LQ of 88.31 (SD = 12.86), while men had a mean LQ of 89.45 (SD = 12.98). There was no sex difference in age, LQ, or years of education (all $t < .93$, n.s.).

All participants had normal or corrected to normal visual acuity and were naïve as to the experimental hypotheses. Participants included students and members of staff who were recruited by announcements and were paid for their participation.

Emotional Faces Task

Emotional faces were taken from the Pictures of Facial Affect Series (Ekman & Friesen, 1976). The images were black and white and measured 313 pixels x 402 pixels. Faces of men and women with neutral expression and expressions of six basic emotions (anger, disgust, fear, happiness, sadness and surprise) were showed. For each emotion, 12 pictures, being 4 males and 4 females (4 repeated posers: 2 males and 2 females), were presented in each visual half field, comprising 12 stimuli for each emotion and 72 for all emotions. Neutral expression comprised 72 stimuli. The stimuli were presented in a counterbalanced order for poser, emotion, and visual half field.

Participants were asked to place their head on a chin rest, at a distance of approximately 57 cm from a monitor, so that 1 cm represents 1° visual angle. To ensure that lateralized stimuli were presented 2.2° visual angle to the left or right of a central fixation cross, participants were instructed to keep their head and body still and to fixate the fixation cross during the whole experiment. All stimuli were presented tachistoscopically for 180 ms in a frame of 3.9 cm width and 5.1 cm height (3.3° and 4.3° visual angle, respectively) with an interstimulus interval of 2 s. The experimental task took about 11 minutes and was run on a standard PC with an Intel Celeron Processor (2 GHz) and a standard 19-inch CRT monitor (Dell, D1226h) operating with a refresh rate of 60 Hz.

Participants were asked to indicate as quickly and correctly as possible whether the presented stimuli showed an "emotional" or "emotionally neutral" face. A trial started with a 2 s presentation of a central fixation cross. Then the stimulus was displayed in the LVF or RVF (in a pseudo-randomized order), while an empty frame appeared simultaneously in the contralateral VHF. Subsequently, participants had to indicate by button press ("Yes" or "No") whether the stimulus was an emotional or neutral face. Two hundred and ninety eight trials were employed by this procedure, the first 10 practice trials were excluded from the analysis. After 144 trials the responding hand was changed in a balanced order. Accuracy (hit rates) and response times (RTs) for correct responses were measured for each VHF.

Results

VHF Emotional Faces Task

Hit rates and median RTs were submitted to a 2 x 2 x 2 analysis of variance (ANOVA), with Emotion (emotional/neutral) and VHF (LVF/RVF) as within-participants factors and Sex as between-participants factor. Geenhouse-Geisser procedure was used with epsilon-corrected degrees of freedom, if data showed significant deviations from sphericity. In case of significant interactions, alpha-adjusted (Bonferroni) posthoc *t*-tests were performed. To avoid inflation of Type I error for multiple comparisons, significance levels was set to $p = .01$.

Right Hemisphere Hypothesis

To test the Right Hemisphere Hypothesis, facial expressions were grouped according to emotional (sadness, anger, disgust, fear, surprise and happiness), and neutral expressions. The 2 x 2 x 2 ANOVA with Emotion (emotional/neutral) and VHF (LVF/RVF) as within-participants factors and Sex as between-participants factor revealed a significant main effect of Emotion, $F(1, 48) = 24.39$, $p < .001$, $\eta^2 = .34$, with higher hit rates for the emotional faces than for neutral faces. The interaction between Emotion and VHF was also significant, ($F(1, 48) = 12.30$, $p < .001$, $\eta^2 = .20$). Paired t-tests revealed a significant LVF advantage for emotional faces ($t(49) = 4.53$, $p < .001$), but no VHF differences for neutral faces ($t(49) = -1.45$, n.s). Moreover, there were higher accuracies for emotional compared to neutral faces in the LVF ($t(49) = 6.25$, $p < .001$), but not in the RVF ($t(49) = 1.99$, n.s.).

In the corresponding analysis for median RTs, the main effect of Emotion was significant, $F(1, 48) = 16.64$, $p < .001$, $\eta^2 = .26$, with faster responses for emotional than for neutral faces. There was also a main effect of VHF, $F(1, 48) = 7.70$, $p < .01$, $\eta^2 = .14$, with faster responses to faces presented in the LVF compared with the RVF. The interaction between Emotion and VHF was not significant ($F(1, 48) = 3.48$, n.s.). Both analyses (hit rates and response times) did not reveal any significant effects involving Sex (all F <2.92, n.s.). Mean hit rates and RTs to emotional and neutral facial expressions for each VHF are presented in Table 1.

Table 1. Mean hit rates and RTs (M ± SD) to emotional and neutral facial expressions presented in the left visual field (LVF) and right visual field (RVF).

		LVF	RVF
Hit rates	Emotion	90.78 ± 6.37	86.67 ± 7.40
	Neutral	81.22 ± 9.40	83.44 ± 8.89
RTs	Emotion	880.6 ± 167.6	919.8 ± 179.8
	Neutral	1041.6 ± 272.7	1045.8 ± 322.9

Valence Hypothesis

To test the original Valence Hypothesis, hit rates were subjected to a 2 x 2 x 2 ANOVA, with Valence (positive/negative) and VHF (LVF/RVF) as within-participants factors and Sex as between-participants factor. Trials with neutral faces were excluded. The analysis revealed a significant main effect of Valence, $F(1, 48) = 61.63$, $p < .001$, $\eta^2 = .56$, with higher hit rates for positive emotions, than for the negative emotions. The main effect of VHF was also significant, ($F(1, 48) = 10.29$, $p < .005$, $\eta^2 = .18$), indicating a LVF advantage. Moreover, the interaction between VHF and Valence was significant, $F(1, 48) = 36.46$, $p < .001$, $\eta^2 = .43$. Simple comparisons revealed a significant LVF advantage for negative emotions, ($t(49) = 6.28$, $p < .001$), but no VHF differences for the positive emotions ($t(49) = -.60$, n.s.).

In the corresponding analysis for median RTs, the main effect of Valence was significant, ($F(1, 48) = 34.93$, $p < .001$, $\eta^2 = .42$), again indicating faster responses for positive emotions. The main effect of VHF was also significant ($F(1, 48) = 12.34$, $p < .001$, $\eta^2 = .20$), indicating an advantage for faces presented in the LVF compared with the RVF. The interaction between Valence and VHF was not significant, ($F(1, 48) = 2.49$, n.s.). Mean hit rates and RTs (M ± SEM) to positive and negative facial expressions for each VHF are presented in Table 2.

Both analyses (hit rates and response times) again did not reveal any significant effects involving Sex (all $F < 1.43$).

Table 2. Mean hit rates and RTs (M ± SD) to positive and negative facial expressions presented in the left visual field (LVF) and right visual field (RVF).

		LVF	RVF
Hit rates	Positive	93.50 ± 6.08	94.17 ± 6.42
	Negative	89. 42 ± 8.26	82.92 ± 8.90
RTs	Positive	848.4 ± 162.9	875.4 ± 186.8
	Negative	896.6 ± 175.1	942.0 ± 183.0

Approach/Withdrawal Hypothesis

To test the Approach/Withdrawal Hypothesis, emotions were grouped according to approach motivated emotions (happiness and anger) and withdrawal motivated emotions (disgust, fear, sadness and surprise), the 2 x 2 x 2 ANOVA for hit rates revealed a significant main effect of Approach/Withdrawal, ($F(1, 48) = 14.58$, $p < .001$, $\eta^2 = .23$), indicating higher hit rates for approach motivated emotions. The main effect of VHF was also significant ($F(1, 48) = 10.82$, $p < .005$, $\eta^2 = .18$), indicating a LVF advantage. Moreover, the interaction between Approach/Withdrawal and VHF was significant ($F(1, 48) = 16.76$, $p < .001$, $\eta^2 = .26$). Simple comparisons revealed a significant LVF advantage for withdrawal motivated emotions, ($t(49) = 6.17$, $p < .001$) but no VHF differences for the approach motivated emotions ($t(49) = .31$, n.s.).

For the response times, a main effect of Approach/Withdrawal was significant, ($F(1, 48) = 31.28$, $p < .001$, $\eta^2 = .40$) with generally faster responses to approach motivated emotions. The main effect of VHF also reached significance ($F(1, 48) = 16.68$, $p < .001$, $\eta^2 = .26$) indicating an advantage in favour of the LVF compared with the RVF. The interaction between Approach/Withdrawal and VHF was not significant ($F(1, 48) = 1.38$, n.s.). Mean hit rates and RTs (M ± SEM) to approach motivated and withdrawal motivated facial expressions for each VHF are presented in Table 3.

Both analyses (hit rates and response times) again did not reveal any significant effects involving Sex (all $F < 2.09$).

Table 3. Mean hit rates and RTs (M ± SD) to approach motivated and withdrawal motivated facial expressions presented in the left visual field (LVF) and right visual field (RVF).

		LVF	RVF
Hit rates	Approach	90.83 ± 7.38	90.41 ± 8.30
	Withdraw	90.75 ± 7.01	84.79 ± 8.13
RTs	Approach	857.3 ± 166.4	903.4 ± 185.3
	Withdraw	903.8 ± 173.9	936.2 ± 181.1

Basic Emotions

For the analysis of basic emotions, hit rates were subjected to a 6 x 2 x 2 ANOVA with repeated measures, with Emotion (anger/disgust/fear/happiness/sadness/surprise) and VHF (LVF/RVF) as within-participants factors and Sex as between-participants factor. A significant main effect of Emotion was revealed (F (1, 48) = 47.67, $p < .001$, $\eta^2 = .50$). There was also a main effect of VHF ($F(1, 48) = 20.18$, $p < .001$, $\eta^2 = .30$). Moreover, the interaction between Emotion and VHF was significant ($F(1, 48) = 21.30$, $p < .001$, $\eta^2 = .31$). Paired t-tests between VHFs revealed a significant LVF advantage for anger, ($t(49) = 2.82$, $p < .01$), fear, ($t(49) = 3.97$, $p < .001$), and sadness, ($t(49) = 9.11$, $p < .001$). Moreover, a RVF advantage was found for happy facial expressions ($t(49) = -3.13$, $p < .005$). Facial expression of surprise only approached significance ($t(49) = 2.60$, $p = .012$) and disgust did not reveal VHF differences ($t(49) = -.88$, $p = .38$). Mean hit rates (M ± SEM) to each specific facial emotion presented in each VHF are displayed in Figure 1.

Figure 1

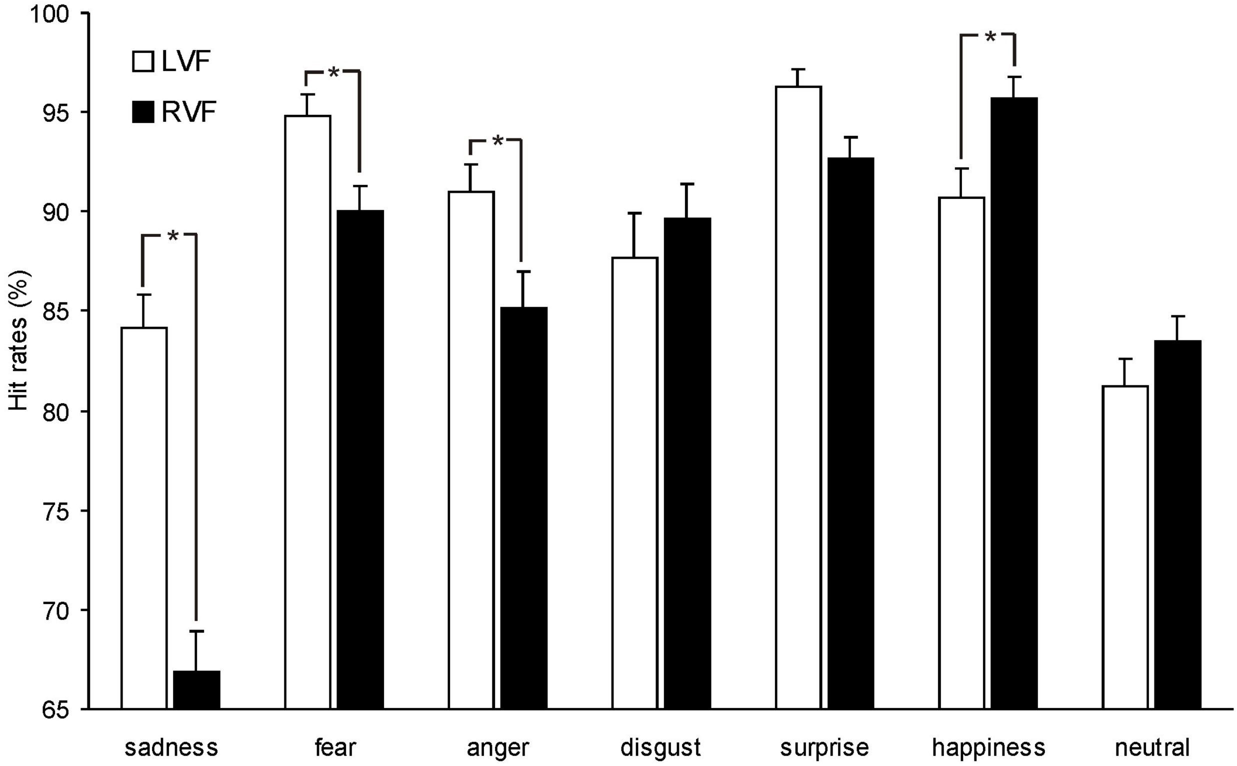

Figure 1. Mean hit rates (M ± SEM) to each specific facial emotion presented in the left visual field (LVF) and right visual field (RVF).

The corresponding analysis for response times also revealed significant main effects of Emotion, ($F(1, 48) = 23.71$, $p < .001$, $\eta^2 = .33$) and VHF ($F(1, 48) = 16.68$, $p < .001$, $\eta^2 = .26$). The significant interaction between Emotion and VHF ($F(1, 48) = 3.69$, $p < .01$, $\eta^2 = .07$) indicated significant VHF differences in favor of the LVF for anger ($t(49) = -5.31$, $p < .001$), and sadness ($t(49) = -2.71$, $p < .01$). Moreover, a marginally significant LVF and RVF advantage was shown for fear ($t(49) = -2.56$, $p = .013$) and happy ($t(49) = -2.03$, $p = .048$) expressions, respectively. Finally, nonsignificant VHF differences were revealed for disgust ($t(49) = -.35$, n.s.) and surprise ($t(49) = -1.23$, n.s.).

Again, neither the main effect of Sex nor any interaction with Sex were significant (all $F < 2.14$).

Discussion

The aim of the present study was (a) to review VHF studies of hemispheric specialization in facial emotion perception and (b) to reevaluate empirical evidence (including findings of the present study) with respect to the Right Hemisphere Hypothesis, the Valence-Specific Hypothesis and Approach/Withdrawal model of emotion perception. Results from the present analysis testing FCAs of specific facial emotions revealed an LVF/right hemisphere advantage for the perception of angry, fearful, sad, and surprise facial expression in at least one of two dependent variables (hit rates and/or mean RT). Only happy faces revealed an RVF/left hemisphere advantage, at least in hit rates. The present study did not reveal any VHF effects for disgusted and neutral facial expressions. In sum, results of the present study did not account for any of the three models without restrictions. The Right Hemisphere Hypothesis predicts a right hemisphere advantage for all emotional faces. However, face stimuli expressing disgust did not show a VHF effect, neither for hit rates nor mean RT. Happy facial expressions even revealed a left hemisphere advantage, which is clearly in contrast to the prediction by the Right Hemisphere Hypothesis. Although the left hemisphere advantage for happy faces rather supports both versions of the valence hypotheses, the positive facial expression of surprise was found to be right lateralized. Even less support has been found for the Approach/Withdrawal model because the right hemisphere advantage for angry faces (assumed to elicit approach motivation) additionally contradicts with this version of the valence hypothesis.

If VHF effects were averaged across all (or a selection of) specific emotional expressions, a LVF advantage was promoted, supporting the Right Hemisphere Hypothesis. This is in line with previous VHF studies showing a LVF advantage for facial emotion perception (Alves et al., 2009; Safer, 1981; McKeever & Dixon, 1981; Suberi & McKeever, 1977; Landis et al., 1979; Strauss & Moscovitch, 1981). The majority studies claiming a right hemisphere superiority for facial emotion perception used only a small number of emotions. Also, these studies face the potential limitation that the right hemisphere advantage was driven by face recognition, given that most of these studies did not show an absence of VHF differences for the perception of neutral expressions. This particular caveat can probably be ruled out in the present study because the present study did not find any VHF differences for neutral facial expressions, suggesting that the right hemisphere advantage for emotional perception is relatively independent from face processing.

In favor of the Right Hemisphere Hypothesis, a functional magnetic resonance (fMRI) study using presentation of chimeric faces showed activation in posterior areas of the right hemisphere for processing both happy and sad emotions (Killgore & Yurgelun-Todd, 2007). Additionally, left middle temporal gyrus activation was detected for happy faces adding support to the Valence-Specific hypothesis. The authors suggested that both models are not necessarily in opposition, but may represent different stages of a more complex emotional system. However, the question of a right hemisphere specialization for emotions in general was restricted to only happy and sad emotions. Overall, evidence from neuroimaging studies supporting the Right Hemisphere Hypothesis is rather sparse (Fusar-Poli et al., 2010; Murphy, Nimmo-Smith, & Lawrence, 2003). Also, support for the Right Hemisphere model comes from a lesion study revealing a relationship between impaired emotion recognition after lesions in right inferior parietal and mesial anterior infracalcarine cortices (Adolphs, Damasio, Tranel, & Damasio, 1996). This study did not find impairments in emotion recognition in patients with lesions restricted to the left hemisphere. However, again only happy and sad facial expressions were tested which provides limited support for the RH model. In contrast, studies examining other basic emotions (apart from happiness and sadness) in patients with unilateral lesion seem to support a “negative (only) valence model” (Benuzzi et al., 2004; Burton et al., 2003; Kucharska-Pietura, Phillips, Gernand, & David, 2003; Weniger & Irle, 2002). For example, Weniger and Irle (2002) used a rating task including facial expressions of the six basic emotions and found that right hemisphere lesion patients rated negative expressions less aroused than left hemisphere lesion patients. A further study revealed that patients with unilateral lesions restricted to the right hemisphere were significantly more impaired in recognizing facial expressions of anger, sadness, fear, disgust, and surprise than patients with left hemisphere lesions (Kucharska-Pietura et al., 2003). Finally, Burton et al. (2003), who investigated recognition of negative facial emotions in unilateral lobectomy patients, found impaired performance in patients who underwent right lobectomy as opposed to patients who underwent left lobectomy.

If none of the models does convincingly predict hemispheric specialization in facial emotion perception, one might speculate that FCAs in facial emotion perception cannot be averaged across specific emotions or valence-specific categories of emotions. This idea has been considered by only a few VHF studies that have examined FCAs for specific emotions (Alves et al., 2009; Asthana & Mandal, 2001; Natale, Gur, & Gur, 1983; Safford & Brandaro, 2010), though only two of them included the six basic emotions (Natale et al., 1983; Safford & Brandaro, 2010). None of these two studies however, have directly compared the three competing models as in the present study. Interestingly, these studies also revealed a LVF advantage for angry faces (Natale et al., 1983; Stafford & Brandaro, 2010) which is consistent with the results of the present study and suggest that anger is processed as a negative emotion compatible with its possible harmful consequences, e.g., aggression (Lazarus, 1991). As in the present study, two of the VHF studies evaluating specific emotions also showed an LVF/right hemisphere advantage for sad faces (Asthana & Mandal, 2001; Natale et al., 1983). Moreover, a superior right hemisphere involvement for the perception of fear is supported by another VHF study (Alves et al., 2009). The LVF advantage reported for the perception of these three negative emotions (anger, fear, and sadness), also consistent with the lesion data cited above (Benuzzi et al., 2004; Burton et al., 2003; Kucharska-Pietura et al., 2003; Weniger & Irle, 2002), suggests that negative emotions are more efficiently perceived through the right hemisphere. Hemispheric specialization for the perception of disgust has been somehow controversial, with one study reporting a LVF (right hemisphere) advantage (Natale et al., 1983), whereas, similar to the present study, Stafford and Brandaro (2010) did not find VHF differences.

Although disgust is associated with an unpleasant state and therefore with negative valence, facial expression of disgust has been also perceived as a funny expression (Fine, 1988; Miller, 1997). This may suggest that the perception of disgust may involve coexisting negative and positive valences that elicit unclear FCA patterns. Concerning the perception of surprise, our results and a previous study (Natale et al., 1983) revealed an LVF/right hemisphere advantage. However, an RVF advantage has also been reported (Stafford & Brandaro, 2010). Surprise involves a startle effect which may trigger a stressful or negative perception. Given that it is also considered to be a positive emotion, however, this may explain the inconsistent laterality findings.

FCAs have also been unclear for the perception of happy faces, with one study (Alves et al., 2009) reporting an LVF/right hemisphere advantage, whereas the results of the present study revealed an RVF/left hemisphere advantage. Alves, Aznar-Casanova and Fukusima, (2009) also found an RVF/left hemisphere superiority for neutral faces. According to the authors, this rather uncommon finding is difficult to explain and might not necessarily indicate a left hemispheric advantage for the perception of neutral expressions but might arise from the specific experimental design. In each trial, the target stimulus (neutral faces) and distractor (emotional faces) were presented simultaneously in the RVF and LVF. If, however, participants applied a response strategy that targeted the easier detectable emotional faces, the apparent RVF advantage for neutral expression might actually reflect a LVF/right hemisphere advantage for emotional face perception in general. In contrast, the present study revealed no VHF differences for the perception of neutral expressions. According with VHF studies examining the perception of specific facial emotions, none of the three proposed models are supported. The data rather suggest a “negative (only) valence model” for facial emotion perception. The lack of support for the Right Hemisphere Hypothesis was mainly based on a consistent LVF/right hemisphere advantage for the perception of anger, fear and sadness but inconsistent for surprise, happiness and disgust. Similarly, data on FCAs between emotions do not follow the valence-specific laterality prediction for happiness, disgust and surprise.

Support for the Approach/Withdrawal model is even less convincing given that only FCAs for the perception of fear, and sadness are compatible with the model.

Our data and the literature supporting a "negative (only) valence model", consistently showed an LVF/right hemisphere advantage for a subset of negative emotions which included anger, fear and sadness. The consistent LVF/right hemisphere advantage for this selection of negative emotions may rely on a common specific attribute of these emotions supporting an "Anger Fear Sad model" (AFS). In fact, marked increases in heart rate were found for anger, fear and sadness which distinguished them from another subset (i.e., enjoyment, surprise) that revealed little change in heart rate, and from disgust, which showed heart rate slowing (Ekman, Levenson, & Friesen, 1983; Levenson, 1992). Although each of these emotions seem to be mediated by specific brain regions, such as the right middle temporal gyrus in fear and sadness (Blair et al, 1999; Morris et al., 1998) and the right orbitofrontal cortex in anger (Blair et al., 1999), their perception may engage an extended right hemisphere neural system (Adolphs et al., 1996). In addition, anger, fear and sadness are particularly associated with the experience of distress, which is linked with heart rate accelerations (Eisenberg & Fabes, 1990). Indeed, the overall performance for response times revealing significantly higher performance in the right hemisphere than the left hemisphere for this particular AFS subset of emotions in the study, support the conjecture that distress-related emotions are more efficiently processed by the right hemisphere. Thus, it might be that an emotional processing system specialized for signaling danger or harmful stimuli (Borod, 1992; Craig, 2005; Fox, 1991) involves right lateralized mechanisms that enable the early allocation of attentional resources to negative stimuli.

Among possible explanations for FCAs it has been argued that brain lateralization is associated with simple computational advantages allowing adaptive strategies (MacNeilage et al., 2009). For example, FCAs has been associated with advantages such as increase in the speed of predator-evasion responses and increase in neural capacity on the basis of specializing one hemisphere for a particular function (MacNeilage et al., 2009). Given that emotions are closely related to the behavior of the individual and its environment, these advantages may also apply to the processing of emotions.

In the present study none of the analyses revealed a significant influence of sex (no main effects and interaction). These findings seem to contradict prior reports of sex differences in FCAs (Bryden, 1982; McGlone, 1980; Harris, 1978; Borod, Koff, White, 1983; Killgore & Yurgelun-Todd, 2001), which also focused on emotional face processing (e.g. Borod et al., 1983; Killgore & Yurgelun-Todd, 2001). A systematic review on VHF studies by Hiscock et al., (1995) reported that 17 out of 92 relevant outcomes show reduced FCAs in females compared to males. An observation that is in line with other reviews and meta-analyses (e.g. Bryden, 1982; McGlone, 1980; Harris, 1978; Hiscock et al., 2001; Voyer, 1996, 2011). However, the effect sizes for sex differences in FCAs seem to be rather small, accounting for only about 1% of the variance in laterality measures (Hiscock, Israelian, Inch, Jacek, & Hiscock-Kalil, 1995) or even less (e.g. Voyer, 1996, 2011). Inconsistencies in the literature on sex differences in FCAs may occur for various reasons. One critical issue is the lack of control of the sex hormonal environment. For example, it has been shown that sex differences in FCAs partly depend on the cycle phase in which female participants were tested (e.g. Hausmann & Güntürkün, 2000; Hausmann, Becker, Gather, Güntürkün, 2002; Weis, Hausmann, Stoffers, Sturm, 2011; Weis, et al., 2008; for review see: Hausmann & Bayer, 2010). Specifically, the majority of these studies suggest that sex differences in hemispheric asymmetries do not exist (or are at least significantly reduced) when women were tested during the menstrual phase. Whether FCAs in emotional facial perception is affected by sex hormones remains still speculative. However, it should be noted that that FCAs in a face-matching task have previously been shown to fluctuate across the menstrual cycle (Hausmann & Güntürkün, 2000). Moreover, there is some evidence that emotional face perception in general is affected by sex hormones (Pearson and Lewis, 2005; Conway et al., 2007; Derntl et al., 2008). For example, higher accuracy for detecting fearful faces was found during late preovulatory phase, when estrogen levels are high, than during menstruation when estrogen levels are low (Pearson and Lewis, 2005).

In sum, the current findings revealed that FCAs for the perception of specific rather than averaged facial emotions do not support the Right Hemisphere Hypothesis, Valence-Specific Hypothesis or the Approach/Withdrawal model. In contrast, this study as well as other VHF studies (Alves et al., 2009; Asthana & Mandal, 2001; Natale et al., 1983; Safford & Brandaro, 2010) and studies on patients with unilateral lesion (Benuzzi et al., 2004; Burton et al., 2003; Kucharska-Pietura et al., 2003; Weniger & Irle, 2002) show that not all basic emotions are equally functionally organized in the brain and only those emotions clearly negative in valence indicate a consistent LVF/right hemisphere advantage.

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